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THE BOTANICAL REVIEW

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CYTOPLASMIC INCLUSIONS OF THE PLANT-LIKE FLAGELLATES. II[1]

R. P. HALL
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During the past ten years, investigations on the plant-like flagellates have included a number of papers on Golgi material and on various types of subcuticular bodies, the latter a relatively neglected group of inclusions. The vacuome and the mitochondria have received less attention, although both types of inclusions have been described in certain species.

GOLGI MATERIAL

The identity of flagellate Golgi material remains somewhat uncertain, since different types of inclusions have been recognized as "Golgi apparatus" in closely related and even in identical species. Recent papers have identified the Golgi material as scattered dictyosomes (14–16), as an osmiophilic cortex of the contractile vacuole (9–11), as osmiophilic bodies applied to the base of the gullet (reservoir) in Euglenida (9), and as osmiophilic globules adherent to the contractile vacuole (10).

Criteria for the recognition of flagellate Golgi apparatus have remained more or less flexible, and the ultracentrifuge (18) has afforded no critical evidence in identification. Positive osmic impregnation has remained the favored criterion. On the other hand, "dictyosomes" have been reported, without successful impregnation, in material stained with iron hematoxylin after osmic fixation (14). In some instances, at least, silver impregnation has proven unsatisfactory (9). Gatenby and his associates have contended that any inclusions which react to vital dyes (*e.g.*, neutral red, methylene blue) can not be considered Golgi material. However, the soundness of this position now seems a bit uncertain in view of Worley's

[1] Supplement to article in The Botanical Review **2**: 85–94. 1936.

(19) apparent demonstration that Golgi material in various invertebrates and vertebrates can be stained supravitally.

The dictyosome-type of Golgi apparatus has been described in *Distigma proteus* (14) and also in certain other Euglenida (15)—species of *Anisonema, Entosiphon, Heteronema, Parastasia, Peranema* and *Petalomonas*. The form of these dictyosomes, constant for a given species, varies from one species to another, although each dictyosome appears double, as if in division (15). Such Golgi bodies are osmiophilic (15), are demonstrable also in hematoxylin preparations (14), are not stainable with vital dyes, and are considered distinct from the vacuome. The number of dictyosomes varies widely with the species—only a single body in *Parastasia grassei* (15), three in *Distigma proteus* (14) and more than 25 in *Heteronema acus, H. mutabile* and *Peranema trichophorum* (15). However, such dictyosomes were not demonstrated in *Euglena* sp. (9, 18) or in *E. viridis* (10). Whether these inclusions are comparable to the previously described "Golgi bodies" of *Euglena gracilis* (1, 2) is uncertain. Similar discrete Golgi bodies have been described in several Phytomonadida—*Eudorina illinoisensis, Pandorina morum* and *Volvox globator* (16)—as dictyosomes which are larger than elements of the vacuome and often appearing as perinuclear crescents with their concavities toward the nucleus.

Golgi material of different types has been described in other flagellates. That of *Chilomonas paramecium* (Cryptomonadida) has been identified as the cortex of the contractile vacuole (11), an interpretation proposed previously by Nassonov. In fission, the osmiophilic cortex is said to become separated from the contractile vacuole and subsequently divided between the daughter flagellates (11). Patten and Beams (18), on the other hand, failed to note impregnation of the contractile vacuole in this species.

The Golgi material in *Copromonas subtilis* (Euglenida) may appear as an osmiophilic cortex of the reservoir, or as an osmiophilic vesicle or a group of osmiophilic granules in contact with a non-osmiophilic reservoir (9). An apparent division of the osmiophilic material, after separation from the reservoir, also has been described. Gatenby and Singh (9) concluded that the reservoir may collapse, disappear completely, and then be replaced by a growing osmiophilic vacuole, the wall of which represents Golgi material. This interpretation is unique, since the reservoir of Euglenida usually seems to

be a permanent structure in flagellated stages and even undergoes enlargement and division during binary fission.

Patten and Beams (18) were unable to reach a definite conclusion concerning the identity of Golgi material in *Euglena* sp. However, Gatenby and Singh (9), after studying the preparations of Patten and Beams, identified the Golgi apparatus of this flagellate as numerous "loaf-shaped" osmiophilic bodies applied to the wall of the "contractile vacuole". Actually the Golgi material figured by these workers appears to lie on the wall of the reservoir, and it is likely that their "large bladder-like structure" in contact with the "contractile vacuole" (9) was merely the contractile vacuole in contact with the reservoir. The Golgi material of *Euglena gracilis* has been described as the osmiophilic cortex of the reservoir, and that of *Euglena viridis* as osmiophilic bodies applied to the wall of the contractile vacuole (10).

VACUOME

In the ultracentrifuge technique (18) elements of the vacuome are stratified with the carbohydrate reserves in *Chilomonas paramecium,* with the paramylum bodies in *Menoidium* sp., and pass toward the centrifugal pole in *Euglena* sp. Since Golgi material was not identified in these flagellates, there was no comparison of vacuome with Golgi material. However, Patten and Beams (18) did not believe that the vacuome should be considered Golgi material.

Positive tests for volutin have been reported for the vacuome in *Chilomonas paramecium* (11, 18), *Copromonas subtilis* (9), *Euglena* sp. (18), *E. pseudoviridis* (5), *E. gracilis* var. *urophora* (8) and *Peranema trichophorum* (6). These observations support the conclusion of Baker (1) and earlier workers.

Brief descriptions of the vacuome have been published for *Distigma proteus* (14), *Entosiphon* sp. (6), *Euglena archaeoplastidiata* (5), *E. gracilis* var. *urophora* (8), *E. pseudoviridis* (5), *E. stellata* (7) and *Scytomonas pusilla* (6). In addition to the typical vacuome of *E. pseudoviridis,* Chadefaud (5) has described a "periflagellar vacuome"—certain swellings of the flagellum anterior to the stigma. Each swelling contains an elongated mass which stains like the vacuome. The vacuome of *E. archaeoplastidiata* is unusual in that the majority of the inclusions lie between the

periplast and the chromatophores, mainly in the equatorial region (5). Some of the vacuoles are larger than the elements of the vacuome usually seen in Englenida, others appear as aggregates of small granules, and some even form branching filaments which may anastomose.

As noted previously (13), various workers have suggested the possible identity of vacuome and Golgi material. This suggestion has met opposition. For example, Gatenby, Singh and Browne (10) find no reason for homologizing these inclusions with Golgi material, although they point out that the vacuome "may stain deeply in osmium tetroxide, and may resist decoloration even longer than the Golgi apparatus (osmiophile material associated with the flagellum vacuole complex)". However, Worley's (19) observations, which indicate that metazoan Golgi bodies are frequently stainable with vital dyes, may have reopened this question of the relation between "vacuome" and "Golgi apparatus".

MITOCHONDRIA

Recent work on mitochondria of flagellates includes the description of small granular mitochondria in *Distigma proteus* (14); granular mitochondria, often aggregated around the nucleus, in *Chilomonas paramecium* (11); rod-like mitochondria, demonstrable by both silver and osmic Golgi techniques, in *Copromonas subtilis* (9); peripheral mitochondria in *Peranema trichophorum* and *Entosiphon sulcatum* (6). In the ultracentrifuge method (18) the mitochondria of *Euglena* sp., in contrast to elements of the vacuome, have shown centripetal stratification.

SUBCUTICULAR INCLUSIONS

Subcuticular bodies, apparently distinct from vacuome and mitochondria, have been described in a number of species. The inclusions may be globular, as in *Euglena archaeoplastidiata* (5), or they may be fusiform rods, as in *Gonyostomum semen* (3, 4), *Euglena amphipyrenica* (5), *E. stellata* (7), *Lepocinclis radiata* (5) and *Peranema trichophorum* (6). The fusiform rods lie perpendicular to the surface in some species, but more or less parallel to the periplast in others. The inclusions may be aligned beneath the cuticular striations, as in *L. radiata* and *E. archaeoplastidiata* (5). In some cases they seem to be attached through the periplast

to the striations and may be carried away with the periplast in plasmolysis of the flagellate (5). Similarly, the "mucus-vesicles" of *Euglena intermedia* (12) seemed to be joined by canals to excretory pores in the periplast.

On the basis of staining reactions, two general types of these inclusions have been recognized (6): iodophilic bodies not stainable with cresyl blue or neutral red, and non-iodophilic inclusions which are stainable with vital dyes. Subcuticular bodies reacting to vacuome stains have been described in *Euglena gracilis* var. *urophora* (8), *E. stellata* (7), *E. viridis* (3) and *Lepocinclis radiata* (5). Iodophilic inclusions have been reported in *Distigma proteus* (14), *Entosiphon* sp. (6), *Euglena archaeoplastidiata* (5) and *Peranema trichophorum* (6). In some instances these inclusions are preserved by mitochondrial fixatives but are destroyed by treatment with dilute acetic acid (5).

According to one viewpoint, these subcuticular bodies of flagellates are to be considered secretory globules stored in the cortex—the "mucus-globules" and "mucus-vesicles" of Grassé and Poisson (12) and earlier workers. Another interpretation is that such inclusions are trichocysts analogous to those of ciliates (3, 5, 6, 11, 17).

In some cases, detailed observations tend to support the latter interpretation. Thus, in *Chilomonas paramecium* (17) the subcuticular bodies are said to be discharged as long threads under certain conditions. In fixed and stained preparations of the same species, threads adherent to the periplast have been interpreted as filaments extruded from the small subcuticular "trichocysts" (11). Comparable trichocysts have been reported in several species of *Ceratium* and also in *Diplopsalis lenticulata, Peridinium tripos* and *Polykrikos Schwartzi* (17). Two varieties of trichocysts have been described in the chloromonad, *Gonyostomum semen* (3, 4)—fusiform trichocysts lying perpendicular to the periplast, and small granular ones, both types showing general distribution in the cortex. Both types of trichocysts are discharged to produce long filaments when the flagellates are treated with cresyl blue. The "trichocysts" of various other flagellates—*e.g., Euglena archaeoplastidiata* (7), *Peranema trichophorum* (6)—do not give rise to filaments, although expulsion of the contents may occur after treatment of the flagellates with solutions of iodin or cresyl blue. The expulsion of discrete

"globules" has been reported in *Euglena stellata* (7) and *P. trichophorum* (6). Such "trichocysts" might conceivably be analogous to the fluid-filled trichocysts of certain ciliates.

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PLANT TISSUE CULTURES. II[1]

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The idea of cultivating excised tissues as a means of studying intercellular and intraorganismal correlations was first clearly formulated in 1902, in a now classic paper by Haberlandt (35). Since that time the field of plant tissue cultures has been reviewed many times (14–16, 39–41, 77, 78, 81, 83, 86–88). The most recent and comprehensive treatment is White's "Handbook of Plant Tissue Culture", published in 1943 (89). The present paper, written as a decennial supplementary literature survey, is intended to bring the subject as nearly as possible up to date, especially to cover in detail the years 1942, 1943 and 1944.

Plant tissue cultures may be divided into four main classes, according to the particular tissues or organs involved: *a*) root cultures, *b*) embryo cultures, *c*) cultures of other members such as stem tips, and *d*) cultures of undifferentiated masses. During the developmental phases of the subject, while methods, nutrients, *etc.*, were matters of prime importance, the first of these classes was, for technical reasons, much more intensively studied than any other (81, 88). This is still true. Roots of a dicotyledonous tree, *Acacia melanoxylon,* have been cultivated for the first time (1). The observed increment rates (*ca.* 1.0 mm. per day) were very much less than those recorded for most herbaceous plants (5.0–20.0 mm. per day). This slow growth rate may be characteristic of trees. There is also the possibility that the experimental methods and nutrients, developed for roots of herbaceous plants, may not be entirely satisfactory for woody plants. These questions remain unanswered. Roots of a monocotyledonous plant, *Zea mays,* have likewise been cultivated for extended periods for the first time (47). Five per cent glucose and an agar substratum were used as compared with the 2% sucrose and liquid medium which seems to be superior for roots of dicotyledonous plants. Robbins has demonstrated a specific morphogenetic response of *Datura* root hairs to light, *in vitro* (68). Bonner has demonstrated an inhibitory effect, reversible by application of *p*-amino-benzoic acid, resulting from treatment of tomato roots with sulfanilamide, sulfapyridine and sulfathiazole (3).

[1] Supplement to article in The Botanical Review **2**: 419–437. 1936.

Robbins found β(-4-methylthiazolyl-5)-alanine capable of substituting for thiamin-thiazole in the nutrition of tomato roots (67). He also showed pyridoxine to be highly specific in its effects in the nutrition of tomato roots (70). Tomato roots were observed to respond to nutrition with thiamin plus pyridoxine but not to thiamin plus glycine, while different strains responded differently to niacin (4). Similar results were obtained elsewhere (11, 12). Roots of pea and of oats were shown to be inhibited by indole-acetic acid at concentrations of 10^{-6} M or more (5).

Although these papers still indicate a considerable interest in method, the major emphasis has shifted from how to grow roots to what can be done with roots when grown. Henderson and Stauffer used excised tomato roots in a study of respiratory processes (38). Thiamin synthesis by maize roots has been demonstrated (47), and synthesis of ascorbic acid by excised tomato roots studied (66). Bonner demonstrated synthesis of thiamin, niacin and riboflavin by roots of a number of species and subspecific strains of plants (2, 4). Dawson has employed the technique in a particularly interesting way as final proof of the localizations of synthesis of nicotine and other alkaloids in roots of tobacco (10), originally demonstrated by means of reciprocal grafts. Hartt has used a similar technique in studying the syntheses and interconversions of sugars in roots of sugar cane (37). The problem of heterotic vigor has likewise been investigated by means of excised root tips (69, 80), while others studied the effects of polyploidy on growth rates of excised tomato roots (71).

The behavior of excised stem tips of sunflower under the influence of a great variety of growth substances has been examined (74). Most substances which promoted rooting or tended to improve the condition of roots when formed showed favorable effects on stem-tip growth, but since these effects generally became evident only after roots were present they were probably indirect in nature. Loo (44) has made a somewhat more clear-cut contribution in cultivating excised stem tips of asparagus *in vitro* for nine months and 20 transfers, studying their organic nutrition.

Although the cultivation of excised embryos is not, strictly speaking, tissue culture, it is so closely related to the cultivation of tissues and has received such a stimulus from tissue culture studies (*vide* the 1944 Conference on Plant Embryo Culture at

Smith College) as to justify its inclusion here. This subject had been touched on cursorily many times in the past four decades (13, 36, 42, 43, 65, 75, 76, 79, 82). Recently there has been a marked increase in such studies. Van Overbeek, Conklin and Blakeslee demonstrated the effectiveness of certain constituents of coconut milk in the nutrition of excised embryos of *Datura* (58, 59), and others made preliminary studies of the chemistry of these constituents (60). Development of embryos in culture, without special reference to their nutrition, has been investigated in *Hordeum* (48). Work with excised embryos of *Iris* (64) and with cabbage (9) has indicated that the seed coat contains an inhibitor which retards germination of the seed. Gregory and his associates (33, 34, 62, 63, 72) studied the vernalisation of excised embryos and parts of embryos of rye, thus segregating the factors affecting the embryo directly from those acting through the endosperm. Loo and Wang have likewise cultivated embryos of conifers (45). The method is beginning to have considerable importance in the study of interspecific hybrids where embryo development is defective for nutritional reasons.

The last class of materials for cultivation, undifferentiated or only slightly differentiated tissue masses, is of especial interest to the author, and it is in this field that the greatest progress has been made during the past few years. This has followed two distinct lines. In this country such studies have been restricted to neoplastic tissues derived initially from one or another of several types of aseptic tumors. Tissue cultures have been isolated from hereditary tumors of *Nicotiana* (84), crown-gall tumors of *Helianthus* rendered bacteria-free by unknown natural means (93) and crown-gall tumors of *Vinca rosea* rendered bacteria-free by heat therapy (92). All three types of tissue cultures have been shown to be transplantable and to produce new tumors in healthy hosts upon implantation (90, 92, 93). Factors involved in controlling differentiation of *Nicotiana* tumor cultures have also been studied (73, 85). The respiration of tissue cultures of tumor tissues (*Nicotiana* and *Helianthus*) has been compared with that of healthy tissues of the same plants (91). The temperature, acidity and sugar-concentration requirements of *Nicotiana* and *Helianthus* tumor tissue cultures have been found to correspond closely to those previously established (86, 87, 88) for tomato roots (38*a*).

Tissue cultures have not been successfully established from any non-tumorous material in the United States.

In France, on the other hand, even under German occupation, the study of tissue cultures from a variety of healthy (non-tumorous) materials has made great progress with many interesting results in the field of morphogenesis. These have come from two laboratories, that of Nobécourt at Grenoble (five papers) and that of Gautheret in Paris (29 papers). Nobécourt's work has dealt with the effects of nutritional factors, especially thiamin and indole-acetic acid (55, 56), on the growth, budding, root initiation and general *in vitro* development of cultures of carrot, artichoke, potato, salsify and *Scorzonera* (black salsify) (53, 54, 57). Gautheret and his students and colleagues have studied the morphogenetic aspects of the problem, especially the rôle of indole-acetic and naphthalene-acetic acids. Thus, Morel has investigated the effect of indole-acetic acid concentration on the development of tissue cultures of grape (52), has shown that such cultures can be grown indefinitely (50, 51), establishing the only true tissue culture (in the restricted sense) of a woody plant so far reported, and has used such cultures for a preliminary study of parasitism of a non-chlorophyllaceous tissue by *Plasmopara viticola* (49). Martin has studied the interrelations between colchicine and naphthalene-acetic acid as factors in the growth of cultures of artichoke (46). Camus has examined the morphogenetic effect of newly formed buds on the orientation of vascular tissues in cultures of endive (8) and has grafted buds from one such culture to another (7). Buvat has utilized tissue cultures in a study of dedifferentiation in a number of plants, especially carrot (6). Plantefol and Gautheret have studied the respiratory processes in tissues of willow and of carrot (61). Gautheret himself has published 15 papers in the past four years. These include a general manual covering the techniques of plant tissue culture (22), three papers on the effects of heteroauxins on growth of various tissues *in vitro* (26, 27, 30), two more papers dealing with tissue polarity, especially polarity in movement of heteroauxin, and the morphological responses which are believed to result from this polarized movement (19, 25), six papers on the general morphogenesis of plant tissue cultures (18, 21, 28, 29, 31, 32), a note on the extended cultivation of tissue fragments of artichoke (20), one on cultivation of very thin slices of artichoke and

carrot (23) and a brief discussion of the bearing of these various findings on the growth-hormone theory of Haberlandt (24). With the exception of one paper on the development of buds on cultures of cambial tissues of elm (25), these are all qualitative. Gautheret and his students, as well as Nobécourt, lay great stress on the importance of indole- or naphthalene-acetic acid on the growth of tissue cultures, considering them impossible without either an external or an internal source of such substances. Gautheret recognizes that these substances are poisons and believes that the neophysiological irritation of such substances is necessary to prevent maturation, differentiation and loss of proliferative capacity in the cells. It is interesting to note that while tissue cultures have been maintained with equal success in the United States without external sources of heteroauxins, these have all been with tumor materials, and there is some evidence that heteroauxin may play a part in the initiation of such tumors (5*a*). If dependence on a heteroauxin is truly a differential characteristic as between tumorous and healthy tissues, it may prove to be of considerable importance. Since none of the French workers has studied any bacteria-free tumor tissue and no non-tumor tissue has yet been successfully grown by the American workers, this remains a matter for speculation. These materials present possibilities which have as yet scarcely been touched.

The problem of Plant Tissue Cultures, like all other problems, has passed of necessity through a series of stages. At the time of the author's first review in 1931 (81) one could only sketch the theoretical outlines of the field, since no really successful cultures had at that time been established. By 1936 (83) some progress had been made with roots and with cambium. In 1941 (86) the method, though by no means fully perfected, was sufficiently established that attention had begun to be turned toward applications in a variety of problems. Today the method is firmly established, methodology is no longer a matter of crucial importance, and we may hope to see the field of questions in which it may aid toward solutions ever widening. The author considers it a matter for personal gratification to have been privileged to span the decade and a half of investigation in this field and to have played a part in its development.

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THE OEDOGONIACEAE. II[1]

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INTRODUCTION

Botanical investigations, like those in other sciences, have suffered immeasurably in the last decade because of the global catastrophe that engulfed us. Relatively few papers dealing with algology have come out of the European countries at war, or from their colonies, since 1940. Reports dealing with the Oedogoniales which have seen the light of day since 1936—the majority of these are from America—have dealt largely with the taxonomy and distribution of the members of the group.

Papers dealing with the Oedogoniales as a whole include a definitive monograph of the North American species (29) and compilations (9, 13, 14). New species in the order have been described in the last decade (1, 3, 8, 11, 12, 15–17, 19–22, 24, 28, 29, 32).[2] The summary table that follows gives the present numerical status of the three genera of the order. Incompletely described or doubtful species are omitted.

Genus	Species	Varieties	Forms
Oedogonium	322	63	21
Bulbochaete	67	8	5
Oedocladium	9	0	0

DISTRIBUTION AND PERIODICITY

Certain delimited geographical areas have been explored more or less thoroughly for Oedogoniaceae, especially the genera *Oedogonium* and *Bulbochaete*. The reports on these investigations are lists of species, annotated analyses of collections, compilations of literature, detailed coverage of local species by descriptions and keys, or some combination of these. To date, since the previous report in The Botanical Review (27), such publications represent parts of China (12–14), Brazil (28), Puerto Rico (31), North Carolina (34), South Carolina (18), Florida (30), Massachusetts (6), Illinois (4), Texas and Louisiana (26a).

[1] Supplement to article in The Botanical Review **2**: 456–473. 1936.
[2] Papers that came to the attention of the writer prior to 1937 are included in the bibliography of Tiffany (29) and are not recorded here.

These reports give additional credence to the generalization that many, if not most, species of *Oedogonium* and *Bulbochaete* are widely distributed in temperate and subtropical freshwater pools, ponds, lakes and streams. The range of the terrestrial species of *Oedocladium* has been extended in the United States to include North Carolina and Florida. Couch (5) found vegetative filaments of a species of *Oedocladium* in Arkansas. Three of the nine described species of this genus are reported from India (1, 24). Only one species, *Oedocladium hazenii,* is aquatic.

Distributional data are still too meager to furnish much definite correlation of species abundance with geographical or environmental factors. There seems to be some indication of a possibility of reference to certain "subtropical", "temperate" and "ubiquitous" forms in the genus *Oedogonium.* The following paragraph (30), however, indicates the difficulty of making any definite classification on such bases.

Over one-third of the species of *Oedogonium* from Florida also occur in other subtropical areas, including Puerto Rico, Mexico, Brazil and the West Indies. Eighteen of these "subtropical forms" occur in Puerto Rico alone. On the other hand, nearly a third of the Floridan species has also been reported from each of the States of Iowa, Illinois, Michigan and Ohio; about one-fourth from Massachusetts; nearly one-half from the Scandinavian countries and Finland; and only ten species are not reported north of the thirty-sixth parallel of latitude in North America.

Most species of *Oedogonium* and *Bulbochaete* are annuals, although collections from tropical and subtropical regions indicate, as was to be expected, that times of sexual reproduction differ from those in regions to the north. In both Florida (30) and North Carolina (33) maximal sexual reproduction occurs in some species a month or two months earlier than in the North Central States. The number of perennials in the warmer latitudes may be quite large, due to vegetative persistence and to repeated formation of zoospores. Indeed, there is some evidence that an occasional species does not reproduce sexually at all.

The distribution of the species of *Oedocladium* presents an interesting problem. In continental United States the genus has so far been reported from southern States bordering the Atlantic and from West Virginia. Its presence in Arkansas (5), perhaps going

back to the period before the Mississippian Embayment, suggests a relation to historical factors. The Indian species have been found at altitudes of 3,000 to 5,000 ft. in the Himalayas. In the United States *Oedocladium* grows at much lower altitudes. The terrestrial species of the genus are almost always found growing with *Vaucheria,* moss protonema, liverworts, or (in India) *Fischeriella* and *Oedogonium.*

A new terrestrial species of *Oedogonium* (*O. terrestre*) has been reported from northern India (22).

CELL STRUCTURE AND REPRODUCTION

Francini (7) described mitosis in *Oedogonium* and considered the nucleolus important in the formation of the transverse wall. Others (10) conclude, on the basis of certain chemical investigations, that some species of *Oedogonium* are more closely related to the higher plants than to other algae. They found only sitosterol in unsaponifiable material, discovered a new phytosterolin, and observed α-carotene.

Most students of the Oedogoniales have used the terms "monecious" and "dioecious" in distinguishing among certain species, depending upon whether the oogonia and antheridia develop on the same or on separate filaments. Since these words have been applied to diploid sporophytes as well as to gametophytes, Blakeslee's suggestion (2) of terms to be used in describing sexual reproduction in cryptogamic gametophytes would appear to be pertinent to the Oedogoniales. The macrandrous species of the group may then be regarded as "homothallic" or "heterothallic" (26), depending upon whether the male and female sex organs appear on the same or different filaments.

Biswas (1) suggests that a simple unbranched terrestrial form of *Oedogonium* might evolve through a poorly branched form of *Bulbochaete* with setae to a fully branched form of *Oedocladium* with setae suppressed to apical caps. *Oedocladium* would thus be considered as close to *Bulbochaete* but as having reached a higher state of evolution. Randhawa (24) contends that it is much more likely that *Oedocladium* and *Bulbochaete* arose independently from *Oedogonium*-like ancestors by acquiring a potentiality for branching.

Sen (25) reports that certain species of *Oedogonium* are important in alkaline waters in ensuring good breeding places for *Anopholes sundaicus.*

Subterranean resting "buds", responsible for perennation of *Oedocladium operculatum,* have been reported (23) in addition to the usual oospores. The intercalary akinetes are full of food, especially starch. The nodal akinetes resemble the "gemmae" first described by Stahl in 1891 for *Oedocladium protonema.* Other dormant bodies are the yellowish-brown parthenospores, described as arrested and transformed oogonia, full of starch and other foods.

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THE CHEMISTRY AND PHYSIOLOGY OF THE PECTINS. II[1]

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In the ten years that have elapsed since the previous review under the above title was written, a very considerable clarification has taken place in the field of pectin chemistry. Pectic acid has been shown (16) to consist of chains of galacturonic acid. The arabinose and galactose commonly associated with pectin preparations is, therefore, not a constituent of the pectic acid itself but rather of associated polysaccharides. Hirst and Jones (4) have shown that protracted extraction of peanut pectin with 70% alcohol removes an araban, while similar extraction of apple pectin yields a mixture of an araban and a galactan. The araban so obtained consists of chains of l-arabofuranose residues linked through the 1–5 positions. Branching occurs freely, the branches being attached through the 2-positions (4, 6). The galactan component has not been studied so industriously. Hirst, however, has studied a galactan from lupine seeds which is made up of *d*-galactopyranose residues linked through the 1–4 positions by β-glycosidic linkages.

The structure of the polygalacturonide chains has been studied by Luckett and Smith (14) who have shown that in citrus pectic acid the chains are most probably made up of pyranose anhydrogalacturonic acid residues linked in the 1–4 positions through α-glycosidic linkages.

Pectic acid possesses only a very slight reducing power and yields no tri-methyl methylgalacturonoside methyl ester after methylation and methanolysis. This indicates that the galacturonic acid chains in it are either extremely long or that the ends are in some fashion protected. The pectic acid of Morell, Baur and Link (16) yielded an apparent chain length of 8–10 galacturonic residues after methanolysis, while that of Luckett and Smith (13) yielded a chain length of 13, as indicated by physical measurements. These values for the chain length of pectic acid are greatly at variance with the estimate of 100 residues per chain arrived at by Henglein and Schneider (3) for dinitropectic acid on the basis of viscosity

[1] Supplement to article in The Botanical Review **2**: 475–497. 1936.

measurements, and are even more at variance with the chain lengths of up to 1,000 residues estimated by the same workers for nitrated pectins. It is probable that in the preparation of methylated pectic acid extensive breakdown of the chain molecules takes place. In addition, it is possible that in native pectin there may be association of chains into larger units, a theory proposed by Kertesz (11) on the basis of measurements on the rate of decrease of viscosity of pectin sols during enzymatic degredation. It is also possible that pectin may contain branched chains, similar to those found in starch (*cf.* 2) and in the gums (6), although no chemical evidence indicating that this is likely has been adduced as yet.

There has long been an interest in the question whether or not a polygalacturonide, as pectin, might arise in nature by oxidation of the corresponding hexosan, in this case galactan. It would now seem unlikely that pectin arises through oxidation of galactan because the pectic acid chains possess a structure different from that of the associated galactan. In pectin the individual residues are connected through α-glycosidic linkages, while in galactan the residues are connected through β-glycosidal linkages. Similarly there has been speculation as to whether araban might arise from decarboxylation of the corresponding polygalacturonide. This is excluded in the present case, since the araban associated with pectin contains furanose residues whereas the pectin itself contains pyranose residues.

The subject of the enzymes which attack pectin has been reviewed by Kertesz (8). Kertesz refers to pectase, the enzyme which de-esterifies pectin, as pectin demethoxylase. The name pectin esterase would, however, seem to be more accurate (12). Pectinase is now termed pectin-polygalacturonase by Kertesz. Methods for measurement of pectic enzyme activity have been proposed (9, 10). Joslyn and Sedky (7) have shown that the pectic enzymes in fruit mashes can destroy 65% or more of the total fruit pectin within 24 hours.

During recent years considerable interest has been shown in the development of wider uses for pectin and pectin products. De-esterification of pectin by any of several methods has been found to result in pectic acid and pectinic acids which form gels at low sugar concentrations, whose salts may find uses (1) as aids in spray drying, for paper coatings, as thickening agents in desserts, pie

fillings or puddings, as latex thickeners or creaming agents, and even as agar substitute in bacteriological media (15). De-esterification *in situ* in the fruit with the aid of the naturally occurring pectin esterase, followed by extraction of the pectinic acids, has been shown (17) to result in products of particularly high viscosity and of good film-forming properties.

While very considerable advances in the chemistry of pectic compounds have been made during the past eight years, no corresponding advance in our knowledge of their physiology has occurred. The mechanism of the formation of pectins is also a subject whose future development will be of interest.

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RECENT DEVELOPMENTS IN FUNGICIDES. II[1] SPRAY MATERIALS—1936–1944

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INTRODUCTION

In this paper the word fungicide will have the same meaning as in the previous paper (46), of which this is a continuation. It will include only those substances which when applied to higher plants in active growth will prevent the development of fungus diseases without serious injury to the treated plants. This definition excludes disinfectants, as defined by Whetzel and McCallan (59), and all materials applied to dormant or partly dormant plant parts or to picked fruits.

The materials discussed must be beyond the laboratory stage of development. It is not the purpose of this paper to list the thousands of materials that have been tested in industrial, State and Federal laboratories. Only those will be considered that have been tested on plants in the field for the determination of phytotoxic as well as fungicidal properties. Those that have undergone only limited preliminary field tests will be mentioned but not discussed.

Bordeaux mixture remains the standard copper fungicide, but the cuprous oxides, basic sulfates, silicates, oxychlorides and others of the so-called "insoluble" group have come into commercial use, chiefly as sprays and dusts for truck crops (65). Manufacturers have greatly improved the physical properties of these materials by decreasing the size of particles.

Lime-sulfur solution and sulfur are still the standard fungicides for the control of such diseases as apple scab (*Venturia inaequalis*) and the powdery mildews (*Erysiphaceae*) affecting many species of plants. Sulfur in quantity is used for the control of peach brown-rot (*Monilinia fructicola*) and scab (*Cladosporium carpophilum*). The sulfurs now used in dusts and sprays cover and adhere better than those formerly used because they are more finely ground and because, by the use of organic "conditioners", the particles are prevented from sticking together (20). The toxicity of sulfurs for powdery mildew is so specific that it is doubtful that any new fungi-

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cide will supplant them for powdery mildew control alone. Silver compounds have shown some fungicidal value but have not come into practical use (40).

Although the coppers and sulfurs are still the important fungicides, developments of the past ten years have been chiefly in the organic field. In fact, the number and diversity of organic compounds surviving preliminary laboratory tests is such that it is difficult to determine which should be selected for field experiments. Research in organic fungicides has been stimulated by the desire of the investigators and plant growers to find better fungicides, by the manufacturers' search for new uses for their products, and by the war-shortage of copper (8, 47). The remainder of this paper will be devoted to developments in this field.

ORGANIC FUNGICIDES

In his previous paper (46) the writer stated: "At the present time none of the organic compounds or their derivatives show promise of taking the place of the standard inorganic fungicides now in use". At present none of them has come into extensive use but some of them give promise of this (8). The properties that a successful fungicide should have are set forth in detail on pages 586 and 587 in the previous paper, where it is stated that "an ideal fungicide should be toxic to the pathogen, noninjurious or even beneficial to the plant sprayed, even after repeated applications, should cause no toxic accumulations in soils, should be nontoxic to men and animals, cheap and easily obtained, nonexplosive, capable of storage without deterioration, noncorrosive, easily made and applied, conveniently handled, capable of covering and sticking well, remaining active over a considerable period of time, and be insecticidal or compatible with the insecticidal sprays without lessening its effectiveness or that of the insecticide". These requirements show why a long period of testing is necessary before a fungicide can be recommended for use on plants and especially on plant parts that are to be eaten. The questions of possible toxic accumulation in soils and possible toxicity to man are not readily answered. This is particularly true of organic fungicides because often there is no previous knowledge of their effects on man, domestic animals, plants and soils. The problem of compatibility with insecticides is complicated by the activities of entomologists in the introduction of new insecticides.

Optimum dosages have not been worked out for any of these compounds. The determination of optimum dosage takes a long time because it is dependent on so many factors, including toxicity to fungus spores, phytotoxicity, and tenacity and stability of residues, in addition to the effects of weather conditions on pathogen and suscept.

At the present stage of development organic fungicides appear to be more specific than inorganic materials in their toxicity to different species of fungi and are effective at much lower concentrations than the inorganic materials. The finished spray is not so bulky and does not form the heavy unsightly residue of Bordeaux mixture, for example. There is less tendency for direct injury to the sprayed plant but a greater tendency to interfere with normal development. For example, vegetative growth may be stimulated to the detriment of fruit or tuber formation, or the maturity and coloring of fruits may be delayed or prevented. Some of them lack the weathering properties of Bordeaux mixture, either because they do not possess inherent tenacity or because of change of composition when exposed to air and moisture. Most of them are expensive to manufacture, but this may be offset by their toxicity to fungus spores at high dilution, sometimes astonishingly high, and by large-scale production. It would seem, however, that as dilution increases there must be a point at which the quantity of toxic material on a given area of a leaf or a fruit would be too small to resist weathering. Also, with higher dilutions, even distribution becomes increasingly important, since the residues would finally become so slight that they could not be expected to disperse toxic substances outside the areas they actually occupy (23). It is possible, however, that the problem of how to deposit highly dilute fungicides in an even tenacious layer may be solved by the use of carriers in which the active ingredients are dispersed or adsorbed.

DERIVATIVES OF THE DITHIOCARBAMIC ACIDS

As a group, derivatives of the dithiocarbamic acids have shown the most promise of producing fungicides that may become commercially important. As indicated by their names, they have a high sulfur content, often 50% or more, and are sometimes referred to as organic sulfur compounds (19).

Tetramethyl thiuram disulfide appears to have been the first of

the group to be tested (38); however, use of derivatives of the acid as disinfestants had previously been patented (18). This compound is highly toxic to fungi but has sometimes caused serious foliage injury when lime as a safener for lead arsenate is used with it. It has, however, controlled apple scab without serious injury (12). It has also controlled brown-rot and gray mold (*Botrytis cinerea*) of sweet cherries (43), but not cherry leaf-spot (*Coccomyces hiemalis*) (22). It has been shown to be an effective spray for the control of damping off (*Rhizoctonia* sp.) of celery (58) and tulip blight (*Botrytis tulipae*) (19). It may be considered as one of the promising fungicides of this group.

The metal dialkyl dithiocarbamates have received extensive investigation (18, 56, 57) and are at present being subjected to extensive field experiments. Of these, ferric dimethyl dithiocarbamate (Fermate) is the most promising and has shown up so well that it has been used to some extent by commercial growers. As obtained from manufacturers, it is a brown powder, only slightly soluble (120 p.p.m.) in water, which goes into suspension readily. It leaves a black residue which is undesirable on fruits approaching maturity. It burns peach foliage when used with lime, presumably because of the formation of a soluble calcium organic salt. On the other hand, it can be used with, or just previous to, oil sprays on apples without risk of injury (21, 30), an advantage not possessed by lime-sulfur and elementary sulfur sprays which cause severe injury when so used. It is unsafe to use Fermate before or just after bordeaux mixture (30), probably because of the formation of the injurious copper salt (18). It has given good control of apple scab (12, 25, 41), apple blotch (*Phyllosticta solitaria*) (10, 11, 12), apple leaf spot (*Physalospora obtusa*) (34) and apple bitter-rot (*Glomerella cingulata*) (12, 13, 30, 55) without serious injury; but, on the other hand, it has been reported as not controlling blotch and bitter-rot (34). In the control of apple cedar rust (*Gymnosporangium juniperi-virginianae*) it has surpassed the sulfur sprays now in use (25, 41, 55). It has controlled pear scab (*Venturia pirina*) without causing serious fruit russet (31) and has shown some promise as a control for pear leaf blight (*Fabraea maculata*) (49). It has been tested with considerable success for the control of brown-rot and gray mold (*Botrytis* sp.) of cherries (9, 41, 42, 43). Applications for the control of these cherry diseases and of

peach brown-rot, made just before harvest, leave undesirable black residues on the picked fruit.

In the control of cranberry field rots (*Guignardia vaccinii* and *Acanthorhynchus vaccinii*) it has been superior to the commonly recommended bordeaux mixture (60).

It has controlled blight (*Coryneum beijerinckii*), rust (*Tranzschelia pruni-spinosae*) and brown-rot of peaches (63), downy mildew (*Peronospora destructor*) of onions (36), and powdery mildew (*Erysiphe cichoracearum*) of cantaloups (36); but it has also been reported as not controlling onion powdery mildew (45). It has controlled tulip blight (19), damping off (*Rhizoctonia* sp.) of young celery plants (58), carnation rust (*Uromyces caryophyllinus*) (51), black spot of roses (*Diplocarpon rosae*) (56), downy mildew or blue mold (*Peronospora tabacina*) of tobacco (2, 3, 32) and bean anthracnose (*Colletotrichum lindemuthianum*) (1). On grape it has given fair control of downy mildew (*Plasmopara viticola*) but no control of powdery mildew (*Uncinula necator*) (52).

It has failed to control early blight (*Alternaria solani*) of potatoes and brown-rot of lemons (*Phytophthora citrophthora*) (36). It has been reported as controlling anthracnose (*Colletotrichum phomoides*) (35, 61) and early blight (53) of tomato.

It has controlled cherry leaf-spot (9), but, because its residues are toxic for only relatively short periods, too many applications need to be made for practical control (22).

It appears to be compatible with the commonly used insecticides and may be applied in dust form, 10%–20% Fermate with 90%–80% filler, such as talc or diatomaceous earth (44).

Fermate has sometimes burned the skin of the face, hands and arms of spray operators, but the burns apparently have not been serious.

The lead and zinc salts of dimethyldithiocarbamic acid with solubilities of 44 and 65 p.p.m., respectively, are also toxic to fungus spores (18), but have not been tested extensively. Their residues, being white, are less unsightly than those of Fermate; but lead, because of its toxicity to man, is an objectionable residue constituent. The lead salt has controlled apple blotch (11) and the zinc salt has controlled apple scab (12, 64) and certain diseases of vegetables (27, 62) but appears to be ineffective against apple bitter-rot (64).

Disodium ethylene bisdithiocarbamate (Dithane, HE–175), an-

other of this group, is also a promising fungicide of recent introduction (7). It is most effective when used in combination with zinc-lime (zinc sulphate and lime) (26). Used in combination with lead arsenate it has given some control of apple scab but has caused serious injury to apple foliage (12). Used alone it has given fairly good control of early blight and late blight (*Phytophthora infestans*) of potato, and when combined with zinc-lime has given remarkable control of these diseases (14, 26, 48). The combination, however, did not control apple bitter-rot (12, 13); perhaps a higher concentration than 1 pound of dithane to 100 gallons of water would have given better results. Dithane, though soluble in water, is said to form an insoluble residue on plants (7).

Morpholine thiuram disulfide is another promising member of this group which, however, has not been tested extensively (5).

DIPHENYLAMINES

Derivatives of diphenylamine have shown some promise but appear inferior to the fungicides now in use. 2,4-diaminodiphenylamine is highly toxic to fungus spores, but its high solubility makes it easily washed off by rains (17).

Thiodiphenylamine (phenothiazine) first attracted attention because of its insecticidal properties. For a time it appeared to be a promising fungicide, but it was soon found to be ineffective except under conditions of light infestation (16, 22). Phenothiazine itself is not fungicidal, but when exposed to light and water it soon becomes oxidized to phenothiazone which is fungicidal. Unfortunately it soon becomes oxidized further to compounds that are not fungicidal (16). If the oxidation of phenothiazine could be stopped with the formation of phenothiazone, or if the process could be slowed down, phenothiazine might become a promising spray for apples. It seriously injures peaches and beans, and when applied too often, delays maturity and coloring of apple fruits. Apple leaves sprayed with it become dark green and glistening. When applied on hot sunny days it burns or increases sunburn when it hits the face, hands or other exposed parts of the spray operator.

CHLORINE DERIVATIVES OF QUINONE AND NAPHTHOQUINONE

Sulfur is a constituent of the more promising fungicides hitherto discussed. Forty-two per cent of Fermate, for example, is sulfur. The most promising of the non-sulfur-containing materials is 2,3-

dichloro-1,4-naphthoquinone (U. S. Rubber 604). This material is a powerful fungicide, even at high dilutions (54), and its residues appear to remain on plants and continue active for a long time. It has given excellent control of apple scab (12) under conditions favorable to the disease, and in the control of apple bitter-rot it has surpassed Bordeaux mixture and Fermate (12, 13). It has not caused injury to peach and apple foliage and to peach fruits, but it has caused occasional spotting of apple fruits (12, 13). These spots appear directly under flecks of the spray residue and are of the same shape. Where the spray is well distributed on the fruit these spots do not appear. They are at first deep green with darker stippling and later turn brown. It is quite possible that this injury could be avoided by an even distribution of the spray over the fruit or by increased dilution. Results indicate that the dilution used, 1 pound in 100 gallons of water, might be increased without too great a loss of toxicity. The black residue is objectionable when applications are made on fruits nearing maturity, and the spray has a tendency to delay maturity and to prevent normal coloring. It has also given excellent control of both the early and late blights of potato (26, 48) and of foliage diseases of tomato (39).

Tetrachloroquinone (Spergon), though a successful disinfestant for certain seeds, has not proved consistently effective as a fungicidal spray. Its toxicity to fungus spores is probably due to the fact that it is a powerful oxidizing agent, and its failure as a fungicidal spray may be attributable to the fact that when spread over leaves and fruit in a thin layer it soon loses its oxidation property by reduction to the corresponding quinol.

Spergon has given good control of cherry brown-rot when applied shortly before harvest, but was not effective in the control of gray mold and leaf spot (22). In California (36) Spergon controlled downy mildews of onion and belladona (*Peronospora* sp.), late blight of tomato, lemon brown-rot, cantaloup powdery mildew, and damping off (*Rhizoctonia* sp.) of young celery plants (58), but in New York it did not control downy mildew of onion (45). It has not been effective in the control of apple scab and blotch or of potato early blight (53), though at one time it seemed promising as an apple spray (50).

OTHER COMPOUNDS

The copper xanthates, successful in preliminary experiments, have not survived field tests (15).

Bismuth salicylate and other salts and derivatives of salicylic acid have given excellent results in the control of tobacco downy mildew in seed beds (6), but the bismuth salt did not control downy mildew of onion (45).

Salicylanilide, recommended for mildew-proofing under the name of Shirlan, has been tested extensively as a fungicide but has not proved successful (4).

Preliminary experiments indicate the possible usefulness of derivatives of pyridine and quinoline and of phenyl-mercuric and quaternary ammonium compounds (24, 28, 29, 33, 37, 64).

With laboratory and field workers testing thousands of organic compounds annually, it seems reasonable to expect that a number of organic fungicides will be in use before another ten years have elapsed, but to what extent they may displace the coppers and sulfurs is anybody's guess. Perhaps we may have an assortment of fungicides, organic and inorganic, some generally useful and others valuable only for the control of particular diseases against which, however, they may be greatly superior to the more generally useful ones.

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THE RELATION OF WEATHER TO FUNGUS DISEASES OF PLANTS. II[1]

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INTRODUCTION

The present review is intended as a supplement to that published in this periodical in 1935 (58), and for that reason much of the previous general introduction to the subject is omitted. It is necessary to explain that the literature on this subject, considered in its widest scope, is so extensive, being approximately one tenth of all mycological and phytopathological papers, that it is desirable to restrict this supplementary review to fungus diseases, chiefly of agricultural and horticultural crops.

Any serious paper on crop diseases almost always has some reference to weather relations or to one or more aspects of this subject, while purely mycological papers frequently include some study of the relation of weather factors to the life cycle of the organism involved. Nevertheless, much of this material is incidental to the main research, and as a result such literature finds small space in the present review. A comprehensive picture of the research on this subject carried out in the last decade is gained from the literature which exclusively deals with one or other aspects of the subject. From the point of view of general training, it is satisfactory to note that many textbooks now deal with this subject in some detail (248). It will be appreciated that in order to understand the complex relation of weather as a whole with the epidemiology of economic crop diseases, the separate component parts of the weather must be analysed in some order. In the following pages will be set out the effects of the weather factors on the production, survival, spread and germination of spores and other structures of fungi and on the initiation and progress of the epidemics they cause.

PREDISPOSING FACTORS

Production of the Means of Dispersal

Most of the information on the effects of environmental conditions on the production of various fungus spores concerns those

[1] Supplement to article in The Botanical Review 1: 497–516. 1935.

forms causing aerial diseases. Certainly some of the earlier papers touch on soil organisms from this aspect, but many of the statements are conjectural and based on the similarity of their life histories to those of the few organisms so far investigated. This shows that there is need for research on the biology of many soil organisms.

Temperature. Temperature is known to affect markedly the rate of infection of host plants and the progress of disease. The incubation period of rust diseases, that is, between initial infection and production of fructifications of the rust, has frequently been reported as affected by differences of temperature. For example, the uredospores of *Puccinia glumarum* are formed at 15° to 17° C. with most races, a temperature not much above that optimum for uredospore germination (230). In Russia a maximum day temperature of 24°–25° C. and a minimum night temperature of 2° C. promotes abundant sori production. The sori ripen quickest at 20° C. (172). In *Puccinia graminis tritici* low temperatures, such as 10° and 0° C., increase the incubation period, favour abundant uredosori formation in some forms and stimulate teleutospore development. These features may be associated with the fact that the mycelium of this rust present in infected plants is as resistant to low temperatures as the host itself (152). In Germany it is claimed that the ripening of perithecia of *Venturia inaequalis* is accelerated by the warmer spring temperatures after March 1st, particularly when the mean daily temperature aggregate reaches 105° C. by the time of perithecial maturity. Records of the pre-ripening period showed a constancy over seven years (104).

Humidity. As might be expected, humidity affects the production of fungus spores, whether in perithecia or in open fructifications. It does not follow that high humidities are always favourable. *Peronospora destructor* on onions (260) and *Bremia lactucae* (181) require 100% relative humidity for development of the conidiophores and conidia, the minima being, respectively, 90% and 96%, while it is reported that conidial formation of *Sphaerotheca humuli* v. *fuliginea* in Japan is reduced at 100% but abundant at 93%–96% relative humidity (91). This reversal of the usual relationship may be explained by the theory that this ascomycete is very sensitive to oxygen requirements, for with a saturated atmosphere oxygen will be reduced. The humidity balance is sensitive especially with

reference to spore germination. Sporangial development of *Phytophthora infestans* is checked by quite brief fluctuations of 5% or more of the relative humidity, the detrimental effects being worse than those caused by much wider fluctuations in temperature (183). In many cases actual water is required for production and emission of the ascospores of very many ascomycetes and this is provided by rainfall. For example, discharge of ascospores of *Nectria galligena* in apple canker is closely associated with the volume of rain and not with other meteorological factors. Leaf scars and other wounds are penetrated in these wet spells, and control may be effected partly by pruning in cold dry spells (19, 167). However, in some cases this production of spores is favoured more by alternating periods of wet and dry conditions than by continuously wet periods, and has been confirmed for *Erysiphe graminis* (29) and *Gnomonia ulmea* (181). Presumably, the final stages in spore production and abscission require a temporary dry condition, and the second supply of water will serve for production of a second batch of spores after the first have been dispersed. The presence of rainwater is also necessary for active budding-off of conidia of *Venturia pirina:* after a good rainfall the surface of infected twigs, which have carried dormant mycelium over the winter, is "literally bathed" in conidia, some of which are drawn in between the scales of swelling buds and serve as a future source of scab (28).

The time of production of spores is another aspect which deserves mention. It is obviously necessary for the optimum conditions for spore production to occur at the right moment and also necessary for them to remain so for as long as possible. In confirmation of this, conidiophores of *Podosphaera leucotricha* are produced in five days (14), but sporangiophores and sporangia of *Peronospora destructor* (260) and *Pseudoperonospora humuli* (257) are formed and matured in one night or in 24 hours. Yarwood has established the fact that the asci of *Taphrina deformans* are formed in the evening of one day, divisions take place overnight and the ascospores mature and are discharged at 8 P.M. on the second day (259). The conidia of other ascomycetes, *Erysiphe polygoni* and *E. cichoracearum, Sphaerotheca pannosa* and *Podosphaera leucotricha,* however, are formed and abstricted during the day (33). Thus failure of the optimum conditions to coincide with the particular stage of development which they normally favour leads to cessation of growth of the fungus.

The manner in which humidity assists in the primary dispersal of sporangia of certain downy mildews is most interesting. In periods of desiccation, presumably of short duration, the sporangiophores of *Peronospora tabacina, P. parasitica, P. geranii* and *Plasmopara halstedi* become distorted, but on the return of higher humidity they straighten out with sufficient force to dislodge the sporangia to some distance; the latter then float away in air currents (186).

Survival of Fungi

The survival of fungi is affected by many factors, such as temperature, moisture content of soil and air, spore structure, light, host stimulation and cultural processes. Many of these factors have been analysed in considerable detail in the earlier papers, and it is only the recent literature that requires summarising.

Moisture. There is little doubt that moisture has a major effect on survival, since it is often found that while the spores, *etc.*, may survive quite low temperatures if they are relatively dry, they soon succumb if wet. There are numerous instances of this fact. Uredospores of *Puccinia dispersa* will survive – 26° C. dry, but rapidly die when moist (133); the thinner-walled conidia of *Bremia lactucae* (209) germinate reasonably well after 16 hours at only 16% relative humidity and the thin-walled conidia of *Piricularia oryzae* resist cold better when dry than when wet, germinating abundantly at low temperatures after being frozen at – 10° C. (1). The conidial stage of *Glomerella mume* in Japan survives – 10° C. for 80 days when moist but 260 days when dry (232). The two latter tropical disease fungi must be conditioned to both dry and hot conditions, and therefore it is not surprising that they survive adverse temperatures when dry. Survival potentials of smuts as measured by spore germination after storage in herbaria has shown that the Tilletiaceae survive longer than the Ustilaginaceae. The bunt species, *Tilletia caries* and *T. foetida,* survived 18 and 25 years, respectively, *Ustilago avenae* and *U. hordei* 12 and 13 years, *Entyloma dahliae* 10 years. It was presumed that maturity at the date of collection was correlated, to some degree, with these results (54), and there may also be morphological or other differences between the two orders to account for this.

Apparently, the sclerotia of basidiomycetes, such as *Corticium,* are more resistant to adverse environmental conditions than those

of ascomycetes, such as *Sclerotinia,* and immersion in water causes a more rapid loss of viability than when left dry (178). No explanation of this fact is forthcoming, and it is open to research to discover whether this is due to structural and physiological differences or to the existence of ecotypes. The sclerotia of *Sclerotinia sclerotiorum* are long-lived enough, lasting 11 years in dry soil (21). In comparison with this, in the U.S.A. the sclerotia of the moniliaceous fungus *Phymatotrichum omnivorum* die rapidly in air-dry soil and are not favoured by very low or high soil moisture content. At a moderate soil moisture content, such as 20–40%, they survive five years (234). With really thin-walled conidia, such as those of *Phytophthora infestans,* it is not surprising that these lose their viability in 30 minutes if allowed to dry, while they stand even high temperatures of 35° C. for four hours, and low temperatures of 1°–2° C. for 48 hours, if kept moist (180). Exposure even to 76% relative humidity destroys the conidia in one hour, and exposure to 86%–94% humidity impairs the germinative capacity (183). It is surprising, therefore, to find that sporangia of *Pseudoperonospora humili* survive a severe drought for one month in the field (146), for there is little evident structural difference between the conidia of the previous fungus and this one. These sporangia (or conidia, according to the method of germination) also lasted nine days on drying, cut hop leaves at temperatures of 18° to 35° C., though death followed in 16 days. On the host tissues, at low temperatures of 5°–10° C. in the dark, the sporangia last 40 days, but once they are separated from the hop leaves they die rapidly. The effect of the host tissues is also shown in increased activity of zoospores in water suspensions (146). It is understandable that oospores of the Peronosporaceae should require ample moisture for germination and that they should be able to survive unfavourable conditions for long periods, owing to their very thick walls. There still remains much to be learned about the dormancy, germination and general biology of these spores, however. Two recent researches on this particular subject concern *Peronospora destructor* and *Pseudoperonospora humili.* The oospores of the former were found to germinate progressively better the greater their age after four years (144). The oospores of the latter germinate over a wide range of temperature after wetting for four to 16 days and require a dormant period of several months. They also survive several years of dry

storage at about 15° C. or at −18° C. (146). In addition, it was observed that oospores of *Sclerospora graminicola* could survive eight years when dry (233).

Temperature. The influence of temperature is nearly as important as that of moisture, and acts in various ways. It is a generally accepted principle that dormancy is initially broken by the increase of temperatures in spring. In some instances, certain spores cannot survive in a dormant condition, but either germinate within a short period or die, *e.g.,* the conidium of *Erysiphe graminis* (29). The perithecia of this fungus are claimed to carry it over the summer rather than over the winter (29), but this assumption is at variance with the opinions of other workers (60) who consider the perithecia as the over-wintering phase. Although the conidia of this fungus are reported as germinating at temperatures up to 35° C. and even in a dry atmosphere, it seems likely that summer conditions in Canada are liable to kill the conidia. On the other hand, in more temperate climates survival of this fungus over the summer is likely to be independent of the perithecia; hence, it is suggested that in hotter climates the perithecia serve to carry the fungus throughout the year, in temperate climates only through the winter. In another hot country, India, it has been found that the conidia of apple scab (*Venturia inaequalis*) lose their germinative capacity very quickly, owing to the high temperatures, and only freshly formed spores generated in spells of lower temperatures of 10°–12° C. are able to germinate (175). No doubt, the perfect stage serves to perpetuate this fungus over the hot summers in India.

It is now well established that the uredospores of cereal rusts have different temperature requirements than those of the teleutospores, and this fact may be correlated with the annual epidemics, the source of the inoculum being in some cases local and in other cases many hundreds of miles distant. Black rust of cereals survives hot climates quite readily by means of its uredospores, but there is a limit to this, since while 8% uredospores survive 44° C. for two days, only 1% survive 50° C. and none at 60° C. (109). The summer temperatures may reach 40° C. (104° F.) in Minnesota and even 47° C. (117° F.) in the shade in India; hence, any prolonged period of very hot weather in those countries is liable to kill the majority of these spores.

In North Carolina the winter temperatures are such that by February no viable uredospores of *Puccinia graminis tritici* remain, in spite of the fresh infections which take place from October to December. The sources of infection each year, no barberry being available as the alternate host, are drifts of wind-blown uredospores from south-westerly States in which these spores can over-winter (235). In north Italy uredospores of this same rust occasionally survive on self-sown wheat or grasses, but usually the winter temperatures are too low to permit this. Therefore, the rust is carried over as teleutospores which infect the common barberry which is common in the alpine districts of Italy (214, 215). This is also the case for black rust in Austria, where also *P. triticina* over-winters in the form of mycelium (6), but *P. dispersa* in the form of uredospores (245).

Many spores which are resistant to low temperatures, as for example the conidia of *Sclerotinia laxa* and *S. fructigena* which survived six months on fruits stored at – 14° to – 18° C., fail to survive for long if they are exposed to alternating cold and warm weather in the open air during winter (25). If conidia of *Sclerotinia fructicola, Plasmopara viticola* and *Venturia inaequalis* are frozen dry, by first lining Dixie cups with ice and then adding dry spores, they will survive – 10° C. very readily and even – 40° C. The galls of *Gymnosporangium juniperi-virginianae* can also be frozen to such temperatures, and remain quite viable over a year, but if a water suspension of the separated spores is frozen, then viability declines in three weeks (84). Some spores can be accustomed to low temperatures by a hardening process, and data on this subject are doubtless of value in countries where very severe winters occur. If the uredospores of *Puccinia graminis* are hardened first for ten or more days at 0° C., they survive very low temperatures such as – 29° to – 40° C. much better than unhardened spores. But such hardened spores were more liable to be killed by daily fluctuating temperatures above and below 0° C. than unhardened spores (152). The uredospores of crown rust of oats (*Puccinia coronata avenae*) are favoured by low temperatures (5°–10° C.), but as the temperature rises fewer spores survive, until above 15° C. at any humidity none survives. These spores are not found to perpetuate this rust from year to year in the U.S.A. (197). Longevity of uredospores, other survival factors presumably being optimum, is influenced by the

date and temperature of formation. Those of *Puccinia triticina* survive longest when formed at 15°–20° C. during the month of May (206).

Cladosporium fulvum has long been known to be favoured by high temperatures and high humidity, but while the conidia are killed by a temperature of 46.5° C. (115–116° F.), they apparently can withstand severe winters and remain viable for a year under really severe adverse conditions (81, 82, 113). Other studies confirm this resistance to freezing of *Cladosporium, Botrytis, Penicillium* and *Fusarium.* In countries where the tomato is grown commercially in the open this resistance is an important factor. Many fungus hyphae are no doubt no more resistant to adverse conditions than thin-walled sporangia and conidia, but such hyphae as those of *Rhizoctonia* and *Ophiobolus* are markedly so. The hypha of *Ophiobolus graminis* was found to survive both 34° F. of frost and marked alterations of temperature between – 20° and 70° F., both in culture tests and in the field (54, 60). However, the mycelium and sclerotia of *Phymatotrichum omnivorum* do not survive – 13° C., even for 24 hours, but while growth is inhibited the fungus is not killed at 5° C. It is considered, therefore, that this disease will be limited in the U.S.A. to areas south of a line marking the minimum air temperature of 23° F. (50). Garrett, however, considers the survival of sclerotia of root fungi to be a complex of many factors, of which the microflora as a whole, soil texture, as well as moisture, temperature and acidity, have their part to play (69). The same is true for spores and mycelium, and Garrett sums up thus: "the greater the physiological heterogeneity in a population of resting spores, the longer is the probable survival period of the parasite" (69). The chief cereal root fungi, *Helminthosporium sativum, Fusarium culmorum* and *F. graminearum,* amongst others, were found in Canada (Alberta) to over-winter naturally as mycelia and conidia. Young germ tubes re-grew after being frozen solid overnight at 6° F., while cultures survived 17 days between 0° and – 50° F. or continuous freezing for three months or repeated alternate freezings and thawings over two months. *Helminthosporium* survived better on the soil surface, but the fusaria better when buried (60).

Gibberella saubinetii is known to grow at a wide range of temperatures, and attacks wheat at high and maize at low temperatures,

following a correlation of cell susceptibility associated with insufficient carbohydrates at those respective temperature ranges. It is therefore surprising to find that this fungus when present in seed barley dies sooner when the grain is stored in the laboratory, while other fungi infecting that grain die more readily when stored in a cooler seed house (212). No evidence is available to explain this. It has already been mentioned that conidia of *Phytophthora infestans* survive high and low temperatures when moist (180), but it has now been shown that water suspensions of zoospores and sporangia of this fungus can be frozen to −6° C. for 24 hours or subjected to fluctuating temperatures (min. of −12° C.) for 14 days, and yet those spores remain viable and able to infect potato leaves (23). In most countries where epidemics of blight occur, it is most unlikely that such low temperatures occur often in spring and at all in summer, but it suffices to indicate that those falls in temperature that are likely to occur will not kill these spores, as other work had already indicated (180). It is possible that the loss of viability of blight conidia, according to Murphy (168) and others, was due to a high loss of water from the conidia or zoospores accelerated by high temperatures. Blight has been reported as overwintering in fields in which a tomato crop had been grown, and it was presumed that the survival was made possible by mycelium present in tomato debris (17). Another instance of probable adaptation to low temperatures is afforded by the uredospores of *Puccinia glumarum* which if produced in the winter months have a higher infective power and remain viable longer than if produced in the summer. Incidentally, it should be noted that Straib considers that over-wintering of this rust is less dependent on the winter hardiness of an infected variety than on the length of life of the old, pendant, autumn leaves as it is affected by soil, weather and nutritional conditions (228). It is also claimed in Italy (44) that the early produced uredospores of cereal rusts do not infect summer-sown wheat but do infect the autumn-sown crops and thus must have a dormant period. This has not been supported elsewhere.

Concerning the survival of smut spores on or in soil, there is a differential response according to the separation of spores. For example, only 11% of *Tilletia caries* spores survive as separated spores in surface soil, but 29% of spores survive if in balls and

45% survive if in whole heads. Further, survival was better on the surface than when the spores were buried in the soil (86). Other smuts behave similarly: *Ustilago zeae* spores survive best on the soil surface, reasonably well if buried in dry soil but poorly in wet soil (16). More recent tests gave these results: spore survival in pure sand at 10 cm. depth was 100% in three years and 50% in five years; at 20 cm. depth it was 10–25% in eight years (128). There was no evidence here whether depth or age was the major factor in reducing the survival rate. It is claimed the viability decreases progressively by using loam, clay and humus instead of sand. *Urocystis tritici* survives best buried deeply, but even there the spores gradually die (80).

Sclerotia of *Sclerotium rolfsii* also vary in their viability when buried in soil: on the surface, at four inches depth in moist soil or at two inches depth in very wet soil survival was satisfactory, but at five to six inches depth in wet soil mortality was very heavy (51). It would seem from the above examples that moisture, particularly if in excess with a consequent lack of aeration, causes the fall in survival rates of many soil inhabitants or invaders.

An interesting analysis of geographical distribution of various parasitic fungi showed that this may be closely correlated with the temperature ranges of the fungi as determined under laboratory conditions (225). For example, *Diplodia zeae,* like many other maize fungi, has a relatively narrow temperature and geographical range, no growth occurring at 10° or 35° C. The species of fungi growing at high temperatures (35° C.) are widely distributed in the tropics, while those with good growth at 10° C. are found in the north temperate regions. *Botryosphaeria ribis* has one of the widest temperature and geographical ranges (225).

Light. Although it may be a little out of place here, it seems desirable to discuss the effect of light, since in addition to its influence on the germination of spores and on infection, it also affects the survival of fungi. A very thorough review of this subject up to 1935 has been published (217), and the following résumé from that paper covers the research up to that date. Both visible and ultra-violet light might prove lethal to mycelium or to spore structures or might stimulate either to growth. The effect depended on the intensities and the wave-lengths involved; also the species of fungi varied individually in their reactions. Small doses of irradi-

ation did not stop growth processes but might have stopped cell divisions. Sporulation and even the shape of spores could be influenced in some instances by irradiation. In general, long exposures to ultra-violet light decreased spore production, but short exposures stimulated the process. The germination of spores was independent of moderate intensities of light, but strong irradiation inhibited it. Pigment in cell walls tended to protect the spores. The lethal effect of irradiation was decreased or slowed down at low temperatures. X-rays and radio-active rays were considered to be more harmful than long waves.

Since 1935 observations and experiments have again confirmed the harmful effects of strong sunlight on sporangia of *Pseudoperonospora humuli,* death following exposure for 24 hours (146) on conidia of *Cladosporium fulvum* (81, 82, 113) and on teleutospores of *Cronartium ribicola,* which were still viable, however, after eight hours exposure (99). Uredospores of *Puccinia glumarum* were found to germinate more rapidly in subdued daylight than in darkness above 15° C., but there was no difference below 15° C., while infection could take place in darkness (230).

Low pressure mercury vapour lamps have been in use for some years to control the development of moulds on stored foods in bakeries, refrigerators, transport waggons, *etc.,* the ultra-violet light emitted being strong enough apparently to stop all growth (73, 77, 96, 134). The peak of lethal action is about 2,250 Å, an amount which it is stated is not found in sunlight at the earth's surface (96). To kill spores and sporidia of *Ustilago zeae* wave-lengths between 3,022 Å and 3,130 Å are required (134). Ultra-violet light was found to inhibit growth of *Sclerotium rolfsii* and *Macrosporium solani,* but after ten hours exposure the fungi recovered and grew normally. An explanation is advanced in the theory that growth hormones become concentrated in the bulbous mycelial tips, so that after a time their presence overcomes the inhibitive effect of irradiation (263). The uredospores of *Puccinia graminis tritici* are only slightly protected by a small amount of pigment, less than the teleutospores possess, and this may explain their liability to be killed by strong sunlight; 10% were found to survive 270 hours of exposure to 500–1,500 foot candles and 75 hours at 7,000 foot candles, but none survived 270 hours at 7,000 foot candles. The sunlight in midsummer in Minnesota is stated to reach 10,000 foot

candles; hence, the expectation of survival in such weather is negligible (109). Similar results have been obtained with uredospores of *Phragmidium mucronatum* (37). Viability of some spores declines more rapidly with white than with red or blue light (109).

Smith's view that some of the effects of unfiltered ultra-violet light were really due to heat has been supported by other workers (37, 68). Research on the effects of ultra-short waves is yet without conclusive results, many organisms being unharmed. While some organisms were killed by exposures to short (8–40 m.) and to ultra-short waves (5.2–10 m.), this effect was removed when the temperature was reduced by using a water-jacket. Apart from that factor, the lethal effect was more rapid the greater the density of the organism and was greatest inside infected cereal grains; hence, it was suggested that such a method might be developed for disinfecting cereal seed grain (239).

It is reported that strong sunlight in Japan depresses the size of the lesions on rice caused by *Helminthosporium oryzae* and by *Piricularia oryzae* (111, 112, 169), but, in view of other records of the effect of temperature, and in the absence of contrary evidence, it seems more probable that the direct cause of this fact is the high temperature associated with the strong sunlight. Use has been made, especially in the Punjab, of the high temperatures associated with the sunlight in May and June in order to control *Ustilago tritici* on wheat. Infected grain is soaked in water for four hours and then exposed to full sunlight for another four hours. Smut was reduced from 15% to nil and from 18% to 0.3%. The maximum shade temperatures in the Punjab approximate 120° F. (140).

As stated by Smith (217), the size of spores is influenced by light, for Harter reports that conidia of *Fusarium caeruleum* and others, on standardised media, are longest with the maximum amount of light and shortest in the dark, a medium length occurring with three hours of daylight (89). This is also confirmed for uredospores of *Puccinia graminis tritici* f. 15, which were longest with 301 foot candles, shortest in glasshouse conditions and intermediate with artificial light sources (152). This is, of course, the reverse of the effect on *Fusarium caeruleum*.

While work in Italy has shown that ultra-violet light inhibits the formation of pustules of *Uromyces appendiculatus* (211), low light intensity delays formation of uredosori of *Puccinia graminis* (152);

the latter conforms with the theory that with poor light conditions the nutrition of the plant is unbalanced, and not enough carbohydrate is manufactured to feed both host and parasite. This was pointed out by Brown (22) who gives a number of references to work on this subject and who indicated that the general effect of light upon a host is to increase its susceptibility to leaf parasites, there being an optimum period of illumination. He quotes Forward as finding that *Puccinia graminis tritici* uredosori are fewer and slower in development when the host is in the dark and that with poor light there is a tendency towards hypersensitiveness in hosts that are normally congenial to the parasites. This has been supported by others for this and other diseases (29, 85, 90, 247). The effect of light on the infection of various hosts by seven rust fungi was tested, and infection by five fungi was found to be reduced by darkness, but two (*Puccinia triticina* and *P. antirrhini*) were unaffected (87). In *P. triticina* it was reported that some wheat varieties have their resistance increased by curtailment of light, others the reverse (92). Later, Hassebrauk supplemented this by stating that in the early stages of infection the resistance of moderately, and sometimes of highly, resistant varieties was reduced by poor light, low temperatures and high humidities, whereas in the middle phase only the appearance of pustules was delayed, and in the latest phase resistance was actually increased (93). Low temperatures will also reduce the resistance of barley to *Helminthosporium gramineum* (114). Again, while infection by one strain of *Puccinia lolii* was reduced by decreased light intensities, another strain was not (87).

Varieties of wheat vary in the stage at which they may be susceptible to various diseases, and often one variety is susceptible in the seedling stage and not in the mature stage. It is thus interesting to note that certain wheat varieties, which beyond the seedling stage appeared resistant to *P. graminis tritici* with normal sunlight, become as susceptible as the seedling stage when shaded (88). Since high temperatures of 29°–33° C. conferred the same degree of resistance as intense sunlight, this situation may involve intense sunlight raising the temperature of the host tissues to that which confers resistance, rather than a lethal action independent of heat. That photoperiodic conditions should affect the degree of infection of plants is to be expected, even though the action is an indirect one

involving the metabolic balance between host and parasite. Variations in the degrees of infection with differences in the length of daylight suggested an experiment with *Cronartium ribicola* in which inoculated plants were exposed to daylight for periods from less than nine hours to more than 17 hours (165). The results were:

No. hours exposed:	above 17,	17,	16,	15,	14,	13,	12,	11,	10,	under 9
Percentage leaf infection:	0,	5,	10,	50,	75,	100,	40,	10,	5,	0

From this Moshkov suggests that immunity from fungus parasites may depend upon changes in the leaves induced by photoperiodic conditions. This seems likely up to a certain point and would agree with the theories of Brown and others. But while an increase up to 100% infection at 13 hours exposure to daylight may be explained on this basis, the progressive decrease in percentage infection above 13 hours is hard to explain except on a basis that the longer the daylight the greater the accumulation of heat or lethal effects of sunlight, neither of which seems reasonable.

Spore Dispersal

In discussing this subject, which is a most vital factor in the epidemiology of any disease, it is necessary to consider it from many angles. Wind and wind-blown rain dispersal of the spores of plant pathogens will normally occur only in the spring and summer months, since, as already discussed, the spores or mycelia which survive the winter period initiate the primary summer, conidial phase. It is true that a number of fungi, chiefly of importance as responsible for human mycoses or allergic troubles, may be active over a great portion of the year, indeed, over the whole year as in the case of *Aspergillus,* and for these wind dispersal is important. It is interesting to note that the genera which have species of interest to plant pathologists were found to have spore production and wind distribution mainly in the spring and summer months, whereas other allergic fungi tend to be distributed over a longer period (13, 38, 48, 49, 188). Though rather foreign to this review, it is of interest to note that the abundance of *Alternaria* and *Hormodendron* spores in analysis of air was correlated with the abundance of *Ambrosia artemisifolia* (48).

The earlier contributions to the study of wind dispersal of spores tended to magnify the distances to which spores were distributed, but recently the view has been expressed that many diseases nor-

mally have only local distribution. A comprehensive review of this subject by Craigie (40) may be utilised as a background for discussing the various factors involved. The earlier work, partly covered by other reviews (57, 58), is surveyed by Craigie. Emphasis has been made on the necessity for a quantitative survey of the spore content of air (40, 78, 79, 222), but such work should be related also to the original spore concentration on the host. For example, Craigie cites the prolific spore production of a barberry bush which may release at any one discharge, under optimum conditions, 70,000,000,000 aecidiospores of *Puccinia graminis*. A fructification of *Polyporus squamosus* may yield 100 billion basidiospores. There have been numerous calculations of this nature of the productivity of fungi (136), but, while there have been detailed mathematical treatments of the dispersal pattern (78, 79, 222), no attempt has been made to correlate the density of a spore inoculum with the observed patterns of spore dispersal at regular distances from that inoculum and with certain environmental states, specifically with certain wind velocities. Stepanoff (222) has certainly drawn attention to the need to take into consideration the abundance of spores at the source when evaluating the danger of this source of infection, but he did not attempt the suggested correlation, which might eliminate the need annually to trap spores at regular distances.

Height of dispersal. Up to 1935 the highest record of vertical spore dispersal was approximately 20,000 feet, but since then the U.S.A. Stratosphere Exploration (1935) results demonstrated that fungus spores and bacteria were present in the air between 36,000 and 70,000 feet (223, 224). Meier and Rogers tested these organisms for viability, and recovered *Macrosporium tenuis* as well as species of *Penicillium, Aspergillus* and *Rhizopus*. These are organisms the conidia of which are small and might well be carried further aloft than many rusts. Also the ubiquity of these allergic fungi (13, 38, 48, 188) may explain their predominance over other fungi in high altitude analyses. Little information had been published prior to 1936 on the conditions at very high altitudes, but Steven's results (224) show that the temperature at about 65,000 feet was – 78° F. Quartz tubes containing seven mould fungi were exposed at the maximum height reached (72,395 ft.), and in spite of the greatly increased danger of death from ultra-violet rays and

from low temperatures (*i.e.*, freezing at least of – 110° F.), five, including *Helminthosporium sativum*, grew normally on return to the laboratory. Unfortunately, no details were given as to the humidity conditions in the exposed quartz tubes: if thoroughly dry, the spores might well survive longer than if moist. Meier and Emmett, following these results, subjected the five fungi which survived the stratosphere exposure to a trial in test tube cultures in which they were exposed to – 78° C. (– 108° F.) for 200 hours: all survived and grew, but again it was not stated whether they survived as spores, mycelia or both (224).

Various rusts were collected in the Nanga Parbat region at heights between 7,500 and 13,500 feet (240). Presumably, conditions would approximate those of the general Himalayan range where even in summer months 53 degrees of frost are common. It is not surprising to find, after this, records of spores of fungi, such as *Peronospora destructor*, surviving at 1,500 feet (176). Since conditions more drastic than the foregoing are unlikely to occur in reasonable proximity to normal areas of vegetation, MacLachan's results with *Gymnosporangium juniperi-virginianae* are readily understood (145). He found that basidiospores of this rust could spread as far as seven to eight miles and were viable up to 2,000 feet, but while the spores were killed within one day in completely dry air or with temperatures over 30° C. at any humidity, the conditions prevailing during wind dispersal were favourable to their survival. The falling-off of spore concentration the further they become dispersed was fulfilled for this rust, and eradication of red cedars within a radius of one to two miles was considered ample to protect pomaceous hosts from infection. Other papers also deal with height of spore dispersal (40, 185, 218). The reduction in spore numbers increases with increasing altitude, as previously reported, but within the first 5,000 feet it is considered that there is as much chance of obtaining a large number of spores at one altitude as at another (40).

Distance of dispersal. While it is true that a number of fungi are distributed by winds over vast distances, the danger of such dispersal invalidating quarantine regulations is considered to be small (142), since only 10% to 25% of parasites covered by those regulations have more than local air dispersal. There are exceptions, no doubt, and unusual winds are known to cause exceptional

dispersal. Allergic moulds have been carried several hundred miles in the eastern U.S.A. at concentrations a hundred times the usual (47, 48), while pear scab dispersal was found in Germany to be influenced markedly by the course of a cyclone, the deep depression in its van creating the necessary conditions for ejection of ascospores and their dispersal in the side currents created by the cyclone (95). In America, Canada and India the cereal rusts' dispersal involves vast distances, in spite of the relatively large size of the spores. For example, Craigie gives numerous instances of the dispersal of cereal rusts over 200, 400 and even 800 miles, often despite considerable natural barriers, such as mountain ranges, lakes and forests (40, 41). That a fair proportion of the spores in the spore showers brought by strong winds from the United States are viable is certain from the fact that crops become infected in direct association with these showers. Crops in Manitoba are infected first, then those of East Saskatchewan and lastly those of Alberta. The work of Mehta and others in India has also given ample evidence of the great wind distribution of black rust spores (148–150). *Cronartium ribicola* is recorded as spreading southwards in California 100 to 125 miles, but sometimes even up to 400 miles. The distribution was found to take place mainly in the upper air strata, and charts of the upper air movements facilitated reasonably accurate forecasts of the southward spread of this rust to *Ribes* in California, outbreaks on this host occurring when the humidity favoured infection (160, 161). What seems likely is that certain geographical formations favour long distance winds of considerable velocities with which this wide dispersal of rusts is associated. Evidence has also been presented of the dispersal of fungus spores 400 miles out to sea from California, the numbers collected falling off with increase of distance from the coast (115, 194). Other studies also have been made (205, 221).

There are many instances of short distance spore dispersal, too numerous to quote fully. Downy mildew of tobacco is distributed by wind, and the conidia of *Peronospora tabacina* have been blown over Lake Erie, a distance of 30 miles. In Holland two experiments demonstrated that loose smut of wheat could be spread by strong winds which carried the spores at the height of the flowering heads when the flowers were open. Light winds allow the spores to be carried in vertical air currents and so lead possibly to a greater

distance of spread (182). In take-all of wheat the ascospores are ejected only during or just after rain, and dissemination by wind is likely to be only local, a matter of a few hundred yards, unless the crop is very young (202, 203). The ascospores of *Sclerotinia sclerotiorum* may be blown several miles, however (21). Splashing rain has always been recognised as an important method of spore dissemination, and recent work has verified this factor in the epidemiology of apple blotch (*Phyllosticta solitaria*) (195) and tulip fire (*Botrytis tulipae*) (9), to take only two cases from many others. While on this subject, the possibility of wind-blown infected leaves serving as a source of infection should not be overlooked, as pointed out for apple blotch (195).

Mechanics and mathematics of dispersal. The problem of the rate of fall of spores is, on the whole, a purely theoretical one, since in nature there can be few occasions when air movement is so restricted as to permit application of Stokes' Law to the measurement of the fall. Gregory (79) has reviewed the subject very thoroughly, has brought together the tables of spore dispersal published by many investigators and has subjected the whole to mathematical analysis. He considers that attempts to calculate dispersal can be done only with reference to non-turbulent air movement and are inapplicable except at the earth's surface. One such theoretical aspect may be mentioned, namely, Buller's claim that elongated spores assumed a horizontal position when falling, which affected the rate of fall. This has been shown not to be necessarily true, since the ellipsoidal conidia of *Erysiphe graminis* and *E. polygoni* fell equally in the horizontal and vertical positions (261).

Any mathematical study of spore dispersal must take into consideration the mode of detachment of spores. Stepanoff (222) divided fungi into three groups: (*a*) those with spores readily detached by winds and light air currents, (*b*) those separated and carried through the air with difficulty and (*c*) those not disseminated by air. Most fungi can be placed in groups (*a*) and (*b*), and to these Stepanoff gave the title "anemochores". Dobbs (46) has classified fungi for their mode of dispersal, and here we are concerned only with his "passive" dispersal group. This was divided into (*a*) spore retainers, (*b*) spore drop-shedders, (*c*) dry spore shedders and (*d*) spore shedders (most fungi). Again, the only groups which concern this discussion are the "dry spore" and the

"spore shedders". Stepanoff investigated the rates of fall of various spores and found that this depended *inter-alia* on the size and structure of the species studied.

Stepanoff also constructed a formula to determine the lines round a source-focus at which equal numbers of spores are deposited. Gregory (79) considered it more appropriate for dispersal calculations to suppose that spore clouds were held in suspension in the air but were diluted by air eddies in the course of the major movements of the air. He gives many figures showing the falling-off of spore concentration with increasing height and with increasing distance from the source of inoculum. For the decrease in spore load at increasing height he uses formulae for eddy diffusivity used in meteorology. The reader is referred to his paper for full details, which cannot adequately be covered in the present general paper, and in which a full bibliography of 89 titles is given, though the more outstanding papers of immediate interest to pathologists are listed here (35, 61, 125, 143, 184, 220, 265).

Another aspect of aerial infection is that of physical barriers. As an example, it has been shown in the case of blind seed disease of ryegrass (*Phialea temulenta*) that even though conditions may be optimum for production and release of ascospores, infection of the flowering heads may be impeded by a densely laid crop. When the soil is thinly covered by young ryegrass, adequate air dispersal of the ejected ascospores from the apothecia on the soil surface becomes possible (179, 253). Further, it is not readily appreciated that even soil fungi may be wind-distributed, and Garrett (63, 69, 174) gives as examples *Fomes noxius* on *Tephrosia* and *Grevillea,* and *Ustulina zonata* on tea and rubber.

GERMINATION

Water. Germination of spores is often dependent on the presence of fluid water, rather than on a water-saturated atmosphere. The uredospores of *Puccinia glumarum* (230), the conidia of *Peronospora destructor* (260), of *Pseudoperonospora humuli* (146), of *Colletotrichum trifolii* and of *Sclerotinia fructicola* (256) need actual films of water for germination. Others, like *Cladosporium fulvum,* may germinate in water and in a saturated atmosphere (81, 99, 113), but, as mentioned earlier, the conidia of *Sphaerotheca humuli* v. *fuliginea* germinate very badly or not at all in water or sugar

solutions, whereas they do so readily at 100% humidity (91). Instances where very high humidity is essential for spore germination, but not free water, are *Sphaerotheca pannosa* v. *rosae* (139), which fails to germinate at 75% humidity, and *Podosphaera leucotricha* (14). Conidia of *Erysiphe graminis* can germinate in a completely dry atmosphere (29), and this is also true for those of *E. polygoni* (20, 256). Whether the conidia of the latter fungus germinated or not, those produced at the lowest humidities soon shrivelled and died, while those produced at 80% were merely smaller, though not so turgid, as those produced at 100% humidity. Also, the growth of the mycelium was reduced by low humidities (256). While these conidia remain attached to the conidiophore there is no mechanism for the passage of oxygen and therefore presumably of water, for it has been demonstrated that the papilla by which the conidium is attached to the conidiophore is the only place where such passage is possible, and this is exposed only after detachment (20).

Temperature. The temperature factor is very intimately associated with germination, but, apart from a few special points, it is not proposed to list details of temperature ranges for the different fungi (see 59, 81, 82, 113, 146, 180, 193, 230, 231, 260). It has already been mentioned that low temperatures may harden spores to extreme exposure; similarly, there is a process of temporarily warming spores to increase their germinative capacity. The uredospores of *Phragmidium mucronatum* germinate better if exposed to 27° C. within eight hours of sowing the spores for a germination test. Held for one hour only at the optimum temperature for germination, 18° C., the spores germinate better when removed to other temperatures (36). It is considered that brief spells of favourable temperatures in the field may induce spore germination on leaves, even when the weather is generally unfavourable and caution is required in applying results of laboratory tests to field problems (36). Sclerotia of ergot (*Claviceps purpurea*) germinate better if they are frozen before placing them at 9°–15° C. Temperatures of 18° C. and above are inhibitive to the germination of these sclerotia but favour perithecial development (130). This fits in with the advance of the season and the development of the fungus. Any unusual capacity of spores to germinate at high temperatures always leads to the danger that a disease when intro-

duced into a fresh area, even though possessing a hotter climate, may readily become established. This danger has been foreseen in the case of *Cronartium ribicola,* 31% of the aecidiospores of which germinate at 28° C. (100).

Microclimate. Some useful information has been published on the microclimate of leaves in relation to disease. Moving air not only directly affects the percentage of relative air humidity but also affects the germination of spores by introducing another undetermined factor. Conidia of *Podosphaera leucotricha* germinate and infect apple leaves only at 100% humidity if the air is moving (43 feet per hour), even a drop to 93% humidity inhibiting germination. In still air germination takes place down to 34% humidity (227). It is possible that in still air gaseous and other excretions from the leaves stimulate germination in spite of less favourable moisture conditions, as it is well known that host extracts stimulate germination of conidia of *Pseudoperonospora humuli* (146) and *Sphaerotheca pannosa* v. *rosae* (262), amongst others. Longrée claims (139) that with the last mentioned fungus there was a very high humidity on the leaf surface, even though the general atmosphere was dry, and that this accounted for activity of the fungus. It is suggested (262) that the factor which favours conidial germination when atmospheric humidity is low, is host stimulation. Further, the temperature of the leaf surface is lower than that of the surrounding air and leads to condensation of moisture on the leaf, thus favouring spore germination (258).

Nutrition. Another complication is that temperature ranges may be altered by nutrition. Phosphates raise the maximum temperature for germination of uredospores of *Puccinia glumarum* by 2°–3° C., while peptone and asparagin do so to a less extent. Carbonic acid gas, at 3% and 6% concentrations, reduces and retards germination at temperatures below 12° C. but increases the velocity and extent of germination at 17°–19° C. (230). It has been claimed that an exact knowledge of spore germination temperatures may be of direct use in control experiments. Control of *Sclerotinia fructicola* by sulphur dusting is stated to be better at 40°–55° F. than at 65°–85° F. which is the optimum range for spore germination (141).

DISEASE INITIATION AND EPIDEMICS

Infection. The effect of the various environmental factors on actual infection has also been studied. Several species of *Erysiphe* (*polygoni, graminis, cichoracearum*) are able to infect their hosts at low relative humidities (25%–55%) (256). With *Sphaerotheca humuli* v. *fuliginea* infection is best at 69% to 96% humidity (91). Infection of lettuce leaves by *Bremia lactucae* takes place only at 100% humidity (181, 209), while that of rice by *Helminthosporium oryzae* cannot take place under 80% humidity (134). Even though germination of the uredospores of cereal rusts may be rapid at low temperatures, the infection process may be much delayed at those temperatures (230). This is confirmed specifically for *Puccinia coronata,* for the development of which and the production of uredosori the plants must be post-incubated at 20° C., even though infection can take place at 0°–2° C. (59). A precise analysis of the various stages involved in infection by *Puccinia triticina* demonstrates the fact that optimum conditions must last for some time to permit critical development of the disease. At 23° C. uredospores germinate in one hour, appressoria are found in three to nine hours (two to eight hours after germination), penetration tubes one hour later. In 24 hours almost all spores form substomatal vesicles and three-quarters have infection hyphae. The lower temperatures delay the initial processes, and once these have taken place it appears that the infection hyphae develop inside the hosts rapidly enough to catch up with the stage of development at higher temperatures. The higher humidities favoured maximum amount of infection (7).

The importance of standardising temperature and other factors when testing wheat varieties and strains of *Puccinia triticina* has been stressed. Apparently, some varieties become more resistant at 6° C. instead of more susceptible, and others in a saturated atmosphere become more susceptible instead of showing the usual increase in resistance (92). Such aberrant varieties lose their resistance when deficient in nitrogen. When conducting susceptibility tests on potato tubers for their blight reaction, it is essential to maintain correct temperatures, that is, temperatures at which the host reaction to invasion (by development of necrotic areas) is at the optimum, namely, 16.5° to 21° C. (166). Another way in which temperature acts is by masking symptoms of actual infection, which is different from suppressing infection. High temperatures of

32° C. over a long period mask the symptoms of *Ustilago striaeformis* on *Poa pratensis*, but the symptoms return on reducing the temperature to 20°–25° C. (131).

Although the physiology of parasitism is outside the scope of this review, a few points should be mentioned, as determinations of temperature, moisture and nutrition may be involved. For example, those diseases which rupture the epidermis, such as rusts, gall-forming diseases and scabs, lead to an increased rate of transpiration, whereas the downy mildews cause only a slight increase. Powdery mildews may, on the other hand, even reduce transpiration by adding protection to the cuticle (98). Respiration rates, independent of those of the parasite, also increase with infection by a powdery mildew like *Erysiphe graminis,* though the rate may decrease after a time (2, 3, 189). Teleutospore formation of rusts is now known not to be initiated by nitrogen exhaustion of the leaves, and the new theory is that the stimulus is the gradual loss of water from rust-infected leaves, accompanied by a rise of nitrogen content. The uredospore stage is not stimulated by a loss of water but is favoured by high humidities (70, 206). High root pressure might well be expected to affect the susceptibility to, and progress of, bacterial diseases (117), but high osmotic values in the parts of maize plants infected with *Ustilago zeae* are associated with the higher degrees of infection (192). The correlation is supposed to be associated with the more luxurious growth of plants having high osmotic pressures. However, wheat varieties with high osmotic pressures were reported as more resistant to *Puccinia triticina,* as also were varieties with small narrow leaves (206); hence, there is no consistent pattern of behaviour in this respect, each disease being specific.

Epidemics generally. Gaumann has summed up the principles of epidemiology thus: It is necessary to have (*a*) large populations of the susceptible host, (*b*) a high epidemiological potential of the pathogen, and (*c*) optimum conditions of weather for the pathogen (71). He might have added, however, a fourth condition, namely, that it is necessary to have conditions which suppress any tendency towards host resistance.

The brown rust of wheat caused by *Puccinia triticina* depends first on survival of sufficient inoculum into the winter period. Hot summer weather may have such a deleterious effect on uredospore

germination, as happened in 1931 and 1934 in Sicily, that no epidemic follows in the next year, in spite of otherwise favourable weather (163). Granted this over-summering of uredospores, Chesters (31) concludes from an analysis of 16 severe epidemics and 17 mild epidemics of this rust that the intensity and virulence of an epidemic in any year are governed by the temperature and rainfall in the period of December to March (April in some areas). He finds that the April–May and the June conditions have little effect. Since temperature and moisture are so near the threshold permitting rust multiplication in the winter period, quite minor fluctuations in these conditions turn the balance favourably or otherwise. When these favourable conditions do exist, the rust increases in the winter by a series of uredo generations. In the spring, fluctuations of these conditions are always within the range favourable to the rust. The period of incubation, of course, may fluctuate according to spring conditions, and forecasts of this period may be made (171), as may also be done for *P. coronifera.* Forecasts were made of epidemics of brown rust in Oklahoma in 1945 and were based on the amount of inoculum (17,000 times as much as in 1944) combined with high temperature records for 23 out of 24 days in March (32). Similar correlations have been found in other areas (147, 156), though in Canada the critical months are later (April–May and July) (41).

Black rust (*P. graminis tritici*) similarly depends on the early season temperature and moisture records, the minimum temperature being the more important, as it controls uredospore germination, prevention of which may delay an epidemic for months or suppress it; the maximum temperature is of secondary importance and the mean of no significance. Rainfall and dews in early spring and in midsummer, when the disease is spreading, are of vital importance (41, 121, 147, 156). Severe epidemics of this rust in the U.S.A. in 1916 associated with warm wet weather in July (108), in Kansas in 1935, 1937, 1938 and 1940 (121, 126, 153) and in Texas in 1935 (8) caused considerable loss and were traceable to temperature and moisture records which favoured initial outbreak and spread.

In the north Caucasus all three wheat rusts (*P. graminis, P. glumarum, P. triticina*) were found to be epidemic with considerable loss of crop, since the climate permitted the overwintering of these rusts, and the abundant rainfall and dew in May and June, coupled

with the high day temperatures of June, facilitated infection and spread (12). Mehta and his colleagues (148–150) have shown that the main source of infection of the principle wheat areas in the plains of India are uredospores blown down from the hill crops, since the teleutospores are scarce, being formed in, or subsequently exposed to, the very high lethal temperatures of April–June. Such infection of barberries as takes place is too late to serve as a source for infecting the commercial crops in the plains. Control therefore consists in suspending cultivation of hill crops for two to three years, until resistant crops are developed, or in destroying self-sown plants and stubble some time before sowing the seed (if this has to be done at all in the hill areas), or in suspending the first crop in April in the Nilgiris and other hill areas and postponing until October the sowing of the main crops in central Nepal.

Little has been said so far about physiological races. Since evidence is accumulating to show that strains or physiological races differ in their relation to environmental conditions, it is imperative to know what effects may be expected when once the strains of any fungus in a given district have been identified, for only then may the danger of epidemics be assessed in relation to the weather which may normally be expected. For example, strains of *Puccinia anomala* vary in relation to temperature, some being less, some being more, virulent at 12° C. than at 22° C. (196). Generally, temperatures higher than the optimum may reduce the vigour of uredosori development, progressively passing with increase of temperature from No. 4 type (very susceptible) to No. 3, to No. 2, to No. 1 and to No. 0 (necrotic flecks) type (118). In addition, varieties of cereals may be grouped according to their degree of fixation to infection types. Three strains of *P. graminis tritici* have been tested on 18 wheat varieties in Canada and found to fall into three groups: (*a*) immunity retained with any condition, (*b*) immunity lost but moderate resistance retained at high temperatures of 80° F., and (*c*) those which become susceptible at the high temperatures but are immune or moderately resistant at low temperatures (119). The importance of this was demonstrated by the fact that the "Kenya" and "McMurachy" varieties were less resistant in the higher temperatures at Minnesota than at Winnipeg. Strains of yellow rust (*P. glumarum*) in Germany have been tested similarly on numerous wheat varieties, but a classification of

varietal reactions was made which is different from that above worked out for black rust, thus: (*a*) summer resistance, increasing with higher temperatures and advancing age, (*b*) susceptible at any time or age, and (*c*) resistant at any temperature above 10° C. The (*a*) group is virtually immune in the growing season but bears abundant pustules in autumn and winter (219). However, susceptibility may be increased by nitrogen starvation or infection with bunt.

Other rust epidemics have also been studied and correlated with weather conditions. Spread of *Cronartium ribicola* was considerable in several States in U.S.A. in 1941 and was associated with warm, wet and cloudy weather. The disease was spread 134 miles by wind from West Virginia to North Carolina (185). A further analysis of the necessary weather conditions was made by Hirt who showed, however, that the general seasonal conditions were not a reliable index to the amount of this rust that might be expected. Each year when epidemics of this rust occurred in U.S.A. the bulk of the infection took place in one or two relatively brief periods of cool, wet weather at a time when abundant freshly produced teleutospores were available. Generally, for infection of pines the most important factor was the abundance and length of duration of rain, while for sporidial production either rain or fog was adequate (101).

Concerning potato blight, most workers confirm Everdingen's rules for predicting outbreaks of this disease in Holland (241), in Argentina (52, 75) and U.S.S.R. (170), but outbreaks in South Carolina are claimed to be less dependent on mean temperature and relative humidity than on the amount and distribution of rainfall in the growing season. It is claimed that epidemics can be predicted according to the early season's rainfall (164). Beaumont, however, claims that in Devon the two days' high humidity rule is sufficient to forecast outbreaks of blight, though high temperature is also necessary (10, 11). It has been possible to map out areas favourable and unfavourable to blight epidemics covering the period mid-August to mid-September, and these were correlated with actual outbreaks in the U.S.A. (4). The importance of chilling is shown to be related to the germination of the sporangia formed in the previous high humidity which must persist for 12 hours to permit infection (42). In Colorado, where normally the hot dry sum-

mers are unfavourable to blight, the occurrence of fog in 1941 and 1942 coupled with the previous heavy winter snows (which facilitated survival of infected tubers) led to outbreaks of blight (207).

The source of blight inoculum has long been debated, and Limasset in France claims that infected tubers may provide that inoculum, the conidia of which may be able to survive the particular micro-climate round that plant, even though the general weather is unfavourable. He points out the importance of distinguishing between susceptibility and receptivity. For example, "Early Rose" is a potato variety which is as susceptible to blight as the variety "Saucisse", but it is much less receptive, as its aerial parts are not luxurious enough to provide the favourable micro-climate (135). In the U.S.S.R., also, Naoumova has found that blight survives one season in the buried infected tuber debris. When such debris is brought to the surface the fungus in it sporulates and serves as a source of inoculum for fresh outbreaks. Diseased leaves and tubers kept dry overwinter were used successfully to infect potato stems, but other material left to overwinter naturally in the field failed to infect healthy potatoes. In spite of this, it is claimed that natural overwintering is possible under some as yet unknown conditions of temperature and moisture (173). Bonde and Schultz, however, have shown experimentally that while infected seed potatoes left in the field over winter may give rise to infected shoots, the latter do not serve as important sources of infection for epidemics. They traced the source of a natural epidemic to a refuse-pile on which blight had developed before spraying had commenced, and they showed that the percentage of infection of the crop decreased with increasing distance from the refuse-pile. They also created an artificial refuse-pile and traced the spread of blight from it with the following results:

Distance from refuse:	100 ft.	200 ft.	300 ft.	400 ft.	500 ft.	600 ft.
Percentage blight:	98%	55%	21%	6%	0%	1%

Similar results were obtained in later experiments (15). Literature on similar correlations of weather with various diseases is very extensive, but only representative papers are cited in the bibliography of this article (18, 19, 55, 82, 83, 97, 102, 110, 126, 137, 154, 158, 168, 210, 213, 226, 252, 267).

SOIL CONDITIONS AND PLANT DISEASES

Garrett (66, 67, 69) has brought together the literature on this subject and has analysed the factors involved in the survival and activity of soil-inhabiting plant parasitic organisms and the diseases they cause. Much of the older literature reviewed by him has been reviewed elsewhere (57, 58). He considers that soil conditions will exert the greatest direct influence upon the organisms which spread in the soil external to the roots of their hosts but indirectly through the physiology of the host upon those organisms which pass their life largely inside the host. He considers that survival of a fungus in the soil is conditioned more by the increase or decrease in the amount of inoculum left in the soil than by direct effect on a given quantity of inoculum. For example, *Phymatotrichum omnivorum* may be left in larger bulk after harvest in neutral or acid soils, and survival of *Ophiobolus graminis* may be favoured by a set of soil conditions unfavourable to its parasitic activity. He points out the influence of competitive microflora on any given pathogen: both *Ophiobolus graminis* and *Helminthosporium sativum* have the same optimum temperature of 25° C. in culture, but in the soil the optima are, respectively, 18° C. and 25° C., shown to be due to masking of temperature effect by antagonism of micro-organisms requiring high soil moisture, such as club root, powdery scab, wart disease, various species of *Phytophthora* and allied organisms, the life histories of which necessitate ample supplies of water; also some *Fusarium* diseases, *Helminthosporium sativum, etc.* The diseases which are favoured by wet seasons but the development of which is independent of high soil moisture and which are stopped by unusually dry seasons, are those caused by *Phymatotrichum omnivorum* on cotton, limited by the amount of rainfall from April to July, and *Ophiobolus graminis* on cereals, limited by weather in the spring months (June–August in Canada, August–October in Australia). The diseases favoured by low soil moisture are potato common scab, most smuts, *Gibberella saubinetii* and some *Fusarium* diseases.

Texture of soil has a considerable influence on soil-borne diseases, and while a few diseases are favoured by heavy soils, most are favoured by light soils. In light soils, both high and low moisture groups of diseases exist, though many of the diseases are favoured by low moisture conditions. This is correlated with the

aeration factor which, however, Garrett considers should not be overestimated, since many diseases are equally affected by soil reaction, itself frequently, but not always, associated with soil texture.

It is very natural that fungi such as *Phytophthora* and *Pythium* should depend so largely on high soil moisture, since the liberation, and especially the spread, of zoospores depends on a sufficiency of water. *Pythium irregulare* attacks and kills red pine seedlings most rapidly at high temperatures and also reasonably quickly at 12° C., but it requires water-saturated soil. The optimum conditions are thus wetness, high temperatures and not too acid a soil (198, 199). *Pythium ultimum,* however, can be very destructive even at 60% soil moisture, provided the temperature is at the optimum of 18°–21° C. (5). *Phytophthora cactorum,* while it needs ample water, also requires aeration, since diseases caused by it are optimum at 96% soil moisture (249). Strains of this latter fungus vary in their temperature ranges, but the moisture factor remains constant; the same water relations hold for *P. parasitica* (236, 250).

Garrett placed many smuts in the low soil moisture group; in addition to his own list *Urocystis occulta* on rye (138) and smut of sorghum (155) could be included. The sclerotia of *Sclerotinia sclerotiorum* have been killed by flooding the soil with water (21), yet high soil moisture is said to favour this fungus, and one can only presume that in this case the aeration factor mentioned by Garrett had a large part to play. These sclerotia are known to survive in dry soil for 11 years. Usually *Actinomyces scabies* is considered a dry-soil organism, but Sanford (204) has found it to be as active in moderately wet soil (39% moisture) as in dry soil (19%). This organism grows well in soil too dry for plant growth (204). None of this cancels the conception that moist, but not wet, down to dry soil, with warm temperatures about 20° C., conduce to severe scab when tubers are growing actively (see 57). That tubers of high vitality are more readily infected has been shown experimentally to be correct in Switzerland (72). Four Egyptian smuts, all recognised as low soil-moisture diseases, are there controlled by planting the host seed in very moist soil, at a shallow depth, and the practice works well where irrigation is carried out. Where the soil surface dries rapidly, the seeds may not penetrate the hard soil on germination; hence, this difficulty is overcome by first soaking the seed, then coating them with mud and then planting (122, 123).

Kramer has provided a survey of the physics of soil moisture which may alter some conceptions on interpretations of the relationship of soil moisture to plant diseases. Gravitational moisture, while it provides the source of water for growth, is not directly related to the ultimate growth rates of plants. What Kramer calls the "field capacity" is of more value in this relation to growth rates, as it approximates the "moisture equivalent" of the soil. The variation in soil type from sand to clay, with various percentages of organic contents, affects the field capacity. The water which lies between the field capacity and the "permanent wilting percentage" is that which is available for plant growth. The nearer the water content of the soil gets to the permanent wilting percentage, the more rapidly does the water become less available. Capillary water movement in the soil below field capacity and above the level of the water table is very slow, and it is supposed that roots obtain water more by growing into contact with the water than by water reaching the roots by its own movement. Little or no water is lost by evaporation below eight to twelve inches depth. One of the most significant claims is that it is impossible to half wet a soil and that it appears practically impossible to maintain intermediate moistures. That is, a part of the soil will be wetter to full field capacity and the rest will be unaffected (129). If we read for "plant" or "root" in the above the word "fungus", it will be realised that such a new conception may explain some of the discrepancies which have occurred in experimental work; it particularly may have reference to field conditions rather than to pot and soil moisture control tanks. In any case the plant pathologist may feel constrained to re-examine experimental results in the light of such information as given by Kramer.

The relation of environmental factors with *Ophiobolus graminis* has been poorly understood until recently, and Garrett gives summaries of the results of experiments by himself, Winter, Fellowes and others up to 1944. It would seem that the disease is severe and widespread in light textured and loose badly compacted soils. Thus a poor seed-bed resulting from too late and hasty preparation, ploughing in of long straw stubble and dry grass, dry ploughing and incorporation of unrotted stable manure, all favour the disease. Wet springs and summers are correlated with the disease, but too abundant moisture is unfavourable and may be related to reduction

of aeration. Any relation of oxygen and carbon-dioxide to the activity of the fungus must concern the rhizosphere, that is, the very immediate neighbourhood of the root system, since conditions in the general soil atmosphere are different from the microclimate of the rhizosphere, owing to root respiration and microbial activity of the latter. (Special papers are 54, 69, 255). Other instances of the different temperature relations of various soil diseases are given in other papers (76, 155, 219, 264).

APPARATUS

An American committee on apparatus used in aerobiology surveyed in 1940 the history of air analysis for microbial population in relation to human and plant pest and disease epidemics (39). Details were given in their report on the more outstanding historical techniques such as Rettger's Air Washer (1910), Owen's Dust Impinger (1922), Stakman's Paddle and Bottle (1923), Well's Air Centrifuge (1933), Well's Impinging Centrifuge (1937), Schmidt's trap, Lindbergh–Meier Sky Hook (1935) and the adaptations devised by Proctor (190, 191), Parker, Christoff, Mehta, Chatterjee and others. A survey also was made of the work and results of the pioneers in air-borne analysis, wind distribution of spores, rates of fall of spores, much of which has been previously, and also here, reviewed. Another recent apparatus is Krogh's microclimate recorder (132) which combines the essential features of a pocket thermohygrograph with the usual meteorological micro-recorder. Apparatus for testing plants for their response to controlled environmental factors, such as temperature, soil moisture, humidity and light, has consisted mainly of adaptations of the basic chambers built by Jones and his colleagues, aiming at saving space and cost. Improvements in fineness of control, in more even distribution of temperature and humidity, and in provision of adequate ventilation have also followed, many of which have not necessarily been described in publications (26, 106, 237, 246, 251).

PRACTICAL APPLICATIONS

Several examples have been given in the preceding pages where knowledge of the environmental effects on fungi or diseases has been utilised to control these diseases either directly or by breeding methods, and further examples may be mentioned here. As re-

ported earlier (58), several countries were fast developing before 1935 spray-warning services with special reference to potato blight, vine mildew and apple scab. The present position of the European continent is not known, but at least some research had continued up to 1943 to determine the date of discharge of ascospores of *Venturia inaequalis*. For example, scabbed apple leaves collected at regular intervals and kept under damp conditions in the laboratory discharged spores a few days before discharge occurred in the orchard; hence, provided a regular collection of overwintered leaves was made, the first date of discharge in the laboratory could safely be used to predict when outside conditions would favour initiation of a scab epidemic (103, 104, 105, 116). Prediction of suitable spraying dates for the control of downy mildew of the vine has received more attention in Europe than any other disease. Recent work has demonstrated that a set of rules drawn up for one district for this purpose could not be applied to all areas with equal success; Müller's formula, successful in Germany, is unsatisfactory in south-west France (208), and the Italian oil-spot method was also unreliable in France. In Italy four superfluous sprays could be obviated by one well-timed spray, made possible by accurate forecasts of the outbreak of this disease (200). It is of interest to note the methods of prediction used in France. The primary outbreak can be estimated by the rainfall in the period November to April and by the stage of host growth and oospore germination of *Peronospora viticola* in spring, while the secondary infections can be determined by the condition and number of the primary infections, the relative humidity, period of rainfall and temperature records before, during and after rainfall (208).

As regards forecasting potato blight epidemics in Great Britain, it was found that Beaumont's five rules could be reduced to two, namely, a minimum temperature of 50° F. or over and a relative humidity of 75% for at least two days. With these two recordings forecasts of blight outbreaks were as satisfactory as when using the previous five rules (10, 11). No practical application of this method for forecasting blight has been practised in Britain, however. In the U.S.A., owing to the large losses caused by this disease at a time when food was of primary importance (25 million bushels of tubers were lost in the Upper Mississippi area alone), a forecasting and spray-warning system was initiated in 1943, reports being sent

in by recorders in ten Federal States and two Canadian Provinces. Apparently, rainfall and temperature records were considered sufficient: 70° F. was the maximum temperature conducive to optimum development of the causal fungus, and in no case was blight virulent where the mean monthly temperatures in June and July were above this figure (157). There is no published evidence that a forecasting system has been used for downy mildew of tobacco (*Peronospora tabacina*), a disease which is important in many countries. In the U.S.A. it is suggested that such a scheme would be both possible and useful, since it is claimed that when the mean January temperature approaches 62° F., the mildew will develop, provided the conditions in early summer are also conducive to infection (162).

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